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HOST-PARASITE-DISEASE RELATIONSHIPS IN A MAMMALIAN COMMUNITY IN THE CENTRAL COAST RANGE OF CALIFORNIA

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INTRODUCTION

Man's relation to and dependence upon other forms of life are nowhere illustrated more vividly than in the field of his health. He has known for some time that certain of his most devastating diseases are transmitted to him by mosquitoes, fleas, lice, ticks, and various vertebrates. He is beginning to realize that in many cases these vectors obtain their initial infections from other vertebrate animals which are the natural hosts of the disease organisms. But although he is aware that many members of the animal kingdom thus form a tremendous disease reservoir which may serve as a continuing source of human infection (Meyer 1931), he is as yet largely ignorant of the complex epidemiological interrelationships which this fact implies. For a number of years the George Williams Hooper Foundation has directed research into various aspects of this problem. Part of the Foundation's program has been an investigation of the host-parasite-disease relationships existing in a natural mammalian community. The following report describes this investigation. No such study pretends to be complete or to do more than scratch the surface of this field of inquiry. However, in reporting on the ectoparasites obtained upon six years from the mammals of a restricted area, we have tried to indicate some of the potentialities that such a community provides for the maintenance and spread of disease organisms dependent upon arthropod transmission.

Throughout this study, attention was focused primarily on the California ground squirrel, *Citellus beecheyi*, which has long been known as a factor in

the epidemiology of plague (Wherry 1908). This squirrel is one of the commonest rodents in California and is usually an important member of any natural community in which it is found; in many areas of the state it is a serious agricultural pest. It was accordingly selected for intensive study to determine its role as a reservoir of disease.

In the choice of a site for this investigation, therefore, important considerations were an abundance of ground squirrels, an absence of human activity which would disturb natural conditions, and accessibility throughout the year. These prerequisites were provided by the environs of the Calaveras Dam, in the Livermore Hills of the central Coast Range, eight miles south of Sunol, Alameda County, California. The terrain is rugged there; some hills reach an elevation of 2000 feet, and the bottoms of some canyons are no more than 500 feet above sea level. Grassland predominates, with trees and brush growing chiefly on the northern exposures and in ravines. The climate of the region is somewhat arid. May, June, July, August, and September are largely rainless, and most of the precipitation occurs in November, December, January, and February. Rainfall in this latter period of the study varied from 17.4 to 25.2 inches per year. Conditions are influenced by the moderate weather prevailing on the coast. High morning fogs are frequent in early summer, and a heavy dew accumulates on the low vegetation nearly every night in April and May. The minimum and maximum temperatures recorded were 19° and 109° F. respectively. Mean monthly temperatures of 65°

or above occur regularly in July and August but are sometimes reached in June and may continue through September. The months of December, January and February average 52° or below. Continuous temperature records for the study area are not available, but mean monthly temperatures based on daily maximum-minimum records from the San Francisco Water Department station at Sunol have been combined with precipitation data gathered at the Dam to provide the accompanying hythergraph (Fig. 1).

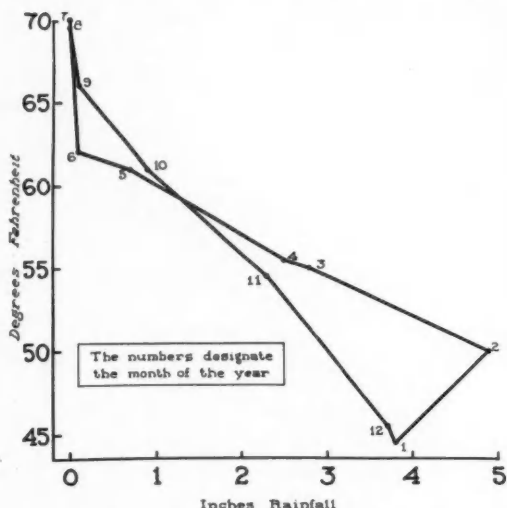


FIG. 1. Hythergraph of weather data for the environs of the Calaveras Dam, Alameda County, California, 1940-45.

The investigation covered about 100 acres on the north and east of the Calaveras Reservoir, adjacent to the Alameda-Santa Clara County line. Intensive work was restricted to an area of approximately 13 acres, of which a more detailed description has been published elsewhere (Evans & Holdenried 1943). The region appeared to be representative of much larger sections of the Upper Sonoran life zone in the central Coast Range. In addition to its ground squirrel population, it supported a considerable mammalian fauna, of which the majority of species came under observation. In view of the many opportunities for the inter-specific exchange of ectoparasites which might be involved in the transmission of disease, the study was broadened to include an examination of as many mammalian hosts and their parasites as possible.

A large-scale program of live-trapping was developed primarily to study the ground squirrels, but many other host species were frequently taken in the traps. Most of them were carefully examined for ectoparasites; the latter were removed and the hosts released after being given suitable permanent identification marks. The various mammals were lightly anesthetized with chloroform before fleas were combed from them into a pan (illustrated in Storer,

Evans & Palmer 1944: 172); ticks, lice and mites were removed singly with forceps. A few dead animals that had been shot or killed by traps or automobiles were also examined.

Field work at the Calaveras Dam began in the spring of 1940 and continued into the fall of 1945. In the first two years the project was not in operation during the winter months, but from January 1943 through August 1944 field observations were made in every month except November 1943 and January 1944. During this time, collections were made from 28 species of native mammals, representing 23 genera, 15 families and 7 orders, as well as from several domestic mammals, five species of birds and three of lizards. Wherever possible, the burrows, roosts or resting places of hosts were examined as well. These sources, which included 2700 mammal examinations, yielded approximately 72,000 ectoparasites. Ectoparasites collected from squirrels especially for plague investigation are not included in this figure. Represented in this ectoparasite fauna were at least 23 species of fleas (Siphonaptera), 12 species of sucking lice (Anoplura), 6 species of biting lice (Mallophaga), 2 species of flies (Diptera), 3 species of true bugs (Hemiptera), 12 species of ticks (Ixodoidea), and 9 species of mites (other Acarina).

To detect the presence of disease organisms in these ectoparasites, it was necessary to triturate many of them in normal saline and to inoculate them into experimental animals (guinea pigs), so that not all of them were identified or permanently preserved. This was particularly true of the ground squirrel parasites. However, a preliminary study of ground squirrel fleas from the Calaveras Dam (Stewart & Evans 1941) had shown that all but a fraction of one per cent belonged to two species, which could be readily distinguished with the aid of a dissecting microscope without being permanently mounted. Most of the subsequent ground squirrel fleas were thus identified by one of us (R.H.). Doubtful specimens, and the fleas of all other hosts, were referred to authorities for identification. Similar experience with the ticks indicated that the majority of them belonged to species which could be recognized in the field while alive or when preserved in normal saline; those that required closer study were permanently preserved in alcohol, and immature forms were sometimes reared to the adult stage. Specimens of all the ectoparasite species recorded were submitted to specialists for determination or verification. An annotated host list of the different species of ectoparasites is given in the Appendix.

This entire six-year project was made possible by the willing cooperation of many individuals. In such a study it is extremely difficult to make categorical separation of the several activities and responsibilities involved. The program was initiated and directed by F. C. Evans until 1941 and the basic outline laid down at that time was, with minor changes, used to complete the study. Subsequent direction was provided by R. Holdenried, who throughout the project did much of the field work and was largely respon-

sible for getting the ectoparasites determined and for compiling the data collected. D. S. Longanecker took over the collection of specimens in the summer of 1942 and continued with the major part of this work until its completion. Preparation of this report has been accomplished jointly by all three of us. Assistance from many other sources, however, has been the real key to the success of this work. We are particularly indebted to the following authorities for their determinations of the various ectoparasite species: J. M. Brennan (Trombididae); A. L. Burroughs (Siphonaptera); R. A. Cooley (Ixodoidea); O. Cope (Anoplura, Mallophaga, Acarina other than Ixodoidea); K. C. Emerson (Mallophaga); D. P. Furman (Laelaptidae); G. P. Holland (Siphonaptera); W. L. Jellison (Siphonaptera, Diptera Anoplura, Mallophaga, Acarina other than Ixodoidea); G. M. Kohls (Ixodoidea); F. M. Prince (Siphonaptera); M. A. Stewart (Siphonaptera); P. Q. Tomich (Siphonaptera); R. Traub (Siphonaptera); R. L. Usinger (Hemiptera); R. L. Wenzel (Diptera); S. F. Wood (Hemiptera). Identification of the less familiar mammal hosts was kindly done by E. R. Hall. For assistance in collecting we are grateful to J. De Lopez of the San Francisco Water Department and to A. L. Burroughs, A. S. Loukashkin, R. Rudd, K. E. Stager and P. Q. Tomich, then associated with the Hooper Foundation. We wish also to thank the San Francisco Water Department for permission to work at the Calaveras Dam. The program has been supported by the George Williams Hooper Foundation, under the able and stimulating direction of K. F. Meyer.

THE GROUND SQUIRREL POPULATION AND ITS ECTOPARASITES

Observations of the population dynamics of California ground squirrels at the Calaveras Dam have already been published (Evans & Holdenried 1943). This species is diurnal, passing the night in its burrows and engaging in foraging and other activities throughout most of the day. When active it stays relatively close to the ground surface and rarely climbs into trees or bushes. It tends to be gregarious, often digging extensive burrow systems. At the Calaveras Dam there was evidence of both estivation and hibernation for varying periods, but not all of the squirrels were inactive at the same time. Breeding took place in the early spring; young were born in April and early May, and nearly all had emerged from their burrows by mid-June. There was normally only one litter a year, which probably averaged six or seven young. As the young squirrels matured, some of them moved away from the areas of the parental burrows; August and September were the months of greatest dispersal. Once established as adult squirrels, many of them spent most of their remaining lives within ranges of less than 150 yards in greatest diameter, with occasional transfers of range to nearby territory. Thus they appeared to have a relatively fixed habitat and a restricted range. Very few squirrels evidently survived more than two years in this area.

FLEAS

Systematic collections of ground squirrel fleas were made in 42 of the 67 months covered in this study. A total of 63,907 fleas were obtained from 2321 squirrel examinations and additional collections were made from their burrows. A preliminary study of approximately 7500 of the fleas (Stewart & Evans 1941) showed that all but about a dozen belonged to two species, *Diamanus montanus* and *Hoplopyllus anomalus*. The collections of subsequent years bore out this observation. These two species have also been found to comprise the bulk of fleas from ground squirrels in other parts of the host range (Evans, Wheeler & Douglas 1943, Linsdale 1946). One individual of *Anomiopsyllus falsicalifornicus* and a few specimens each of *Pulex irritans*, *Opisodasys nesiotus*, and *Orchopeas sexdentatus* were found on squirrels at various times of the year, but never more than one specimen at a time. Two other species, *Atyphloceras multidentatus* and *Monopsyllus wagneri*, were represented by single specimens collected in the burrows and were not taken from the squirrels themselves. Other than *D. montanus* and *H. anomalus*, none of these is truly a ground squirrel flea, and they obviously played an insignificant role in the ground squirrel flea fauna.

The preliminary flea survey (Stewart & Evans 1941) also demonstrated that *H. anomalus* was the most abundant species in the flea fauna of ground squirrels during the summer months, while *D. montanus* was predominant at other times. This phenomenon has been found to be true of ground squirrel flea populations on the Hastings Reservation, Monterey County, California (Linsdale 1946). A similar shift in the species composition prevailed among the ground squirrel fleas at the Calaveras Dam in each of the six years studied (Figs. 2, 3). During the winter months *H. anomalus* virtually disappeared from the ground squirrels; the highest monthly average (the average number of fleas per squirrel capture, based on all captures for a given month) from January through March was 1.3 fleas per squirrel, obtained in January 1943. In April *Hoplopyllus* began to increase from the winter low, but it was not until July that it definitely and consistently outnumbered *Diamanus*. Through the hottest and driest season of the year (July, August and September) *H. anomalus* usually averaged 20 or more fleas per squirrel; the maximum monthly average occurred in August 1942, with 32 fleas per squirrel. There was some variation from year to year in the averages for a given month, but the phenomenon of rising to a marked peak in the summer and declining to a low in winter was constant. *D. montanus*, on the other hand, reached its peak of population density in the winter months. From April to October, when the mean monthly temperatures were 55° F. or above, the monthly average number of *D. montanus* per squirrel ranged from 5 to 17. In October, as the days became definitely cooler and the first rainstorms occurred, the number of *Diamanus* appearing on individual squirrels increased. From October through March the monthly averages ranged from 10 to 58

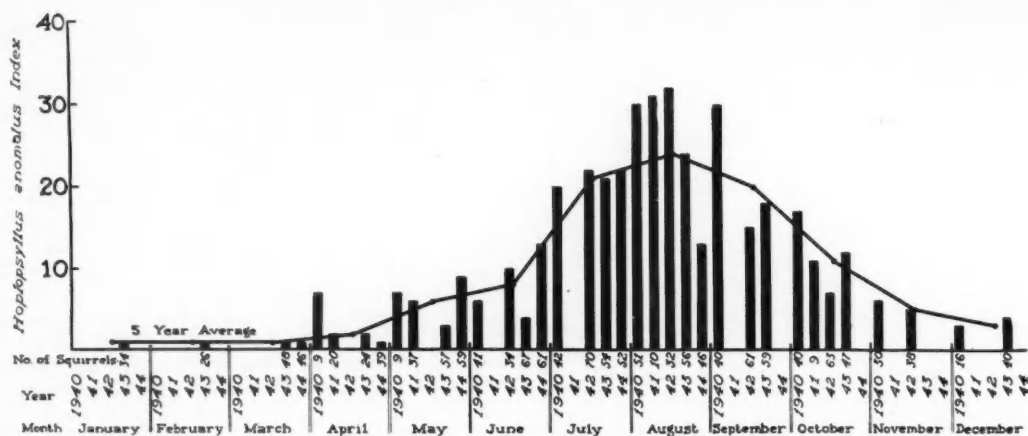


FIG. 2. Average numbers of *Hoplopsyllus anomolus* per squirrel for each month of the investigation, Calaveras Dam, 1940-44.

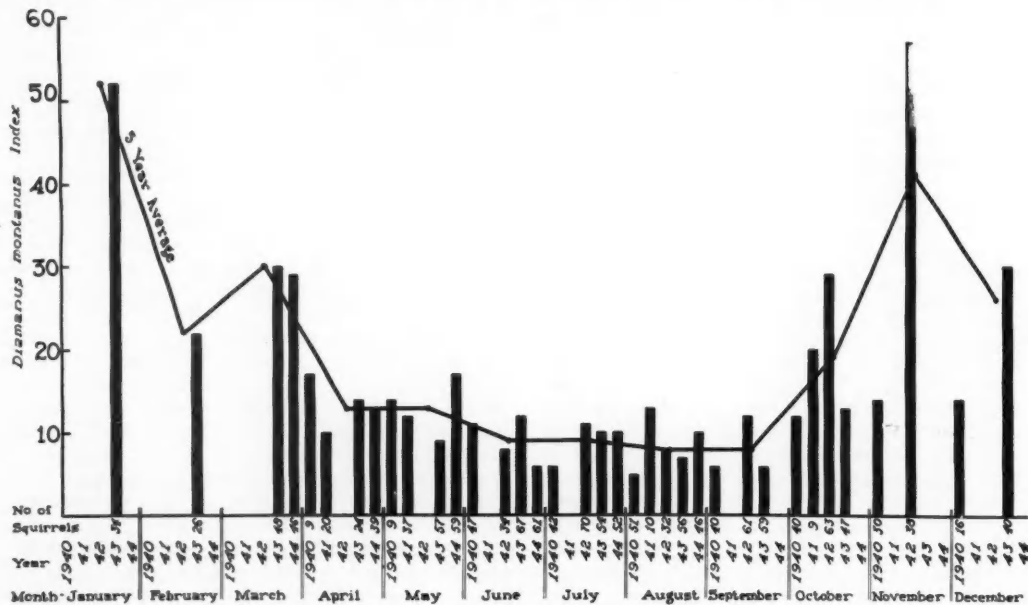


FIG. 3. Average numbers of *Diamanus montanus* per squirrel for each month of the investigation, Calaveras Dam, 1940-44.

fleas per squirrel. The peak of *Diamanus* density was usually reached by December. In addition to reaching its peak at a different time of year, the *D. montanus* population attained a higher maximum than that of *H. anomolus* and did not fall to as low a minimum. The two species evidently have different environmental requirements and seem to react to conditions of the environment independently of one another.

Both *D. montanus* and *H. anomolus* are capable of transmitting plague, although the former is considered to have a higher transmission potential (Wheeler & Douglas 1941). Since the chances of

transmission are presumably greater with a higher flea density, the combined flea index may be of interest (Fig. 4). Fewest fleas per squirrel were found in April, May, and June. This is the transition period between the cool rainy winter months and the hot dry summer; it is also the time when the young squirrels are born and the period in which they are restricted to the nest. This low point in total flea density is the result of a decline in *D. montanus* without any compensating rise in *H. anomolus*. An increase in the latter species during the summer brings about a rise in total flea density so that by August, when the young squirrels are actively dispersing, the

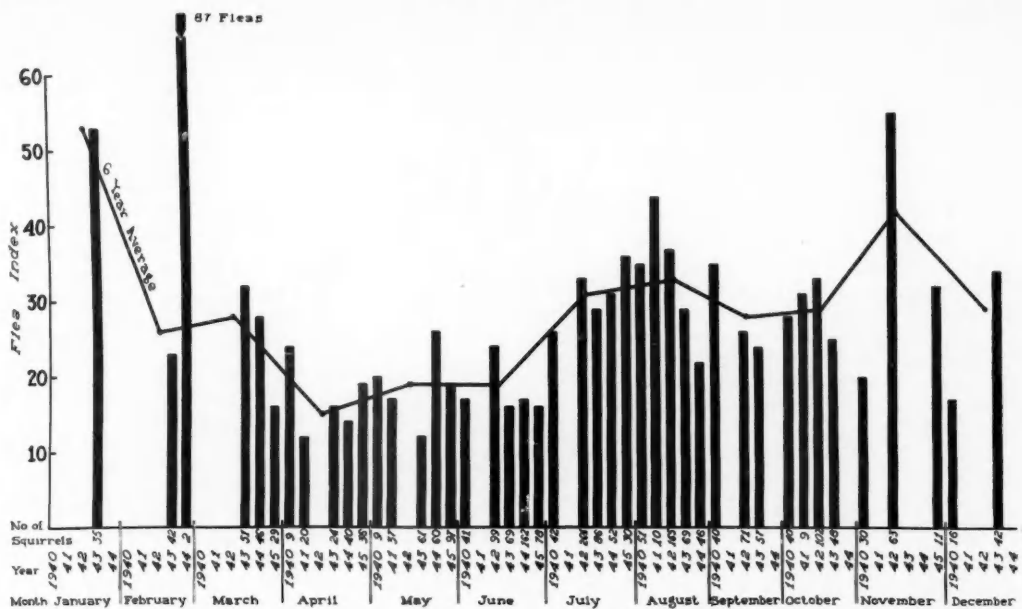


FIG. 4. Average number of fleas per squirrel for each month of the investigation, Calaveras Dam, 1940-45.

number of fleas per squirrel shows a marked increase over that of the spring. Little change in total flea density is seen in the autumn, for the decrease of *H. anomalus* is compensated for by an increase in *D. montanus*. The higher flea densities of the winter were due to *Diamanus* and occurred at that time of year when the squirrels spent more time in their burrows and less time outside. This high density continued into February, at which time most, if not all, of the squirrels were presumably active and had emerged from hibernation. The coincidence of a high flea density and a period of increased host activity would seem to provide conditions suitable for the outbreak of a flea-borne epizootic. Other factors are evidently also involved, for there were no apparent plague outbreaks at the Calaveras Dam during the time of our study.

A factor possibly affecting the density of parasites is any variation which may occur in the number of available hosts. The ground squirrel population at Calaveras Dam experiences a sharp annual increase in the spring, through the more or less simultaneous birth of the young squirrels. The marked summer increase in the flea index began soon after the young had emerged from the burrows. However, the squirrel population then declined continuously from its late spring peak until the following season of birth, but a corresponding decrease was not observed in either the total flea index (Fig. 4) or in the separate indices for *Hoplopyllus* and *Diamanus* (Figs. 2, 3). Thus there was no clear correlation of the host population with that of its flea parasites.

Variations in the sex and age structure of the host population might have some effect upon the density of parasites. The combined flea index for each sex

of young and adult squirrels is shown in Figure 5. In March the adult females averaged 23 fleas each, but in April the number was only 7. The average infestation of the adult males, which apparently did not occupy the nests used by the adult females with young, showed a similar decrease but remained somewhat higher than that of the adult females. Young males also had a higher average infestation than that of young females. This was evident even in June, when both sexes of young were inhabiting a single burrow and presumably shared the same nest. The slightly smaller size of the females may have correspondingly limited their flea-carrying capacity, but this is unlikely. Skin and hair conditions of the male ground squirrel may be more favorable for flea feeding, so that the parasites would remain longer on this sex than on the female and thus larger numbers would accumulate. It is also possible that after family groups have broken up and the various individuals have taken up separate burrows and nests the ecological conditions surrounding the males might favor larger flea numbers. Greater mobility on the part of males, which was observed in the young squirrels but not in the adults (Evans & Holdenried 1943), would also facilitate the acquisition of larger numbers of fleas.

Extreme age of the host did not tend to favor an undue increase in its flea fauna. At the Calaveras Dam, a four-year-old squirrel was rare and much beyond the average age of the adult population. Three squirrels of this age were examined for fleas, and none was found to have unusually large numbers.

It is commonly believed that sick or otherwise abnormal animals are particularly susceptible to parasite infestation. Ailing or under-developed squirrels

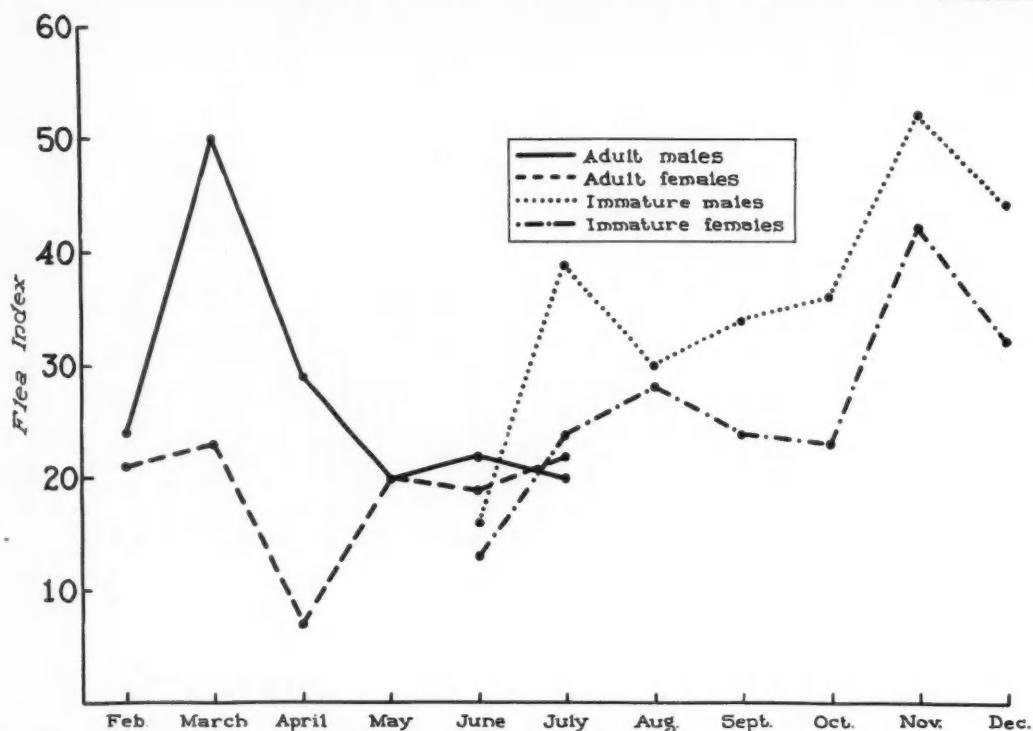


FIG. 5. The combined flea index for young and adult squirrels of each sex, Calaveras Dam, 1940-45.

sometimes had unusually high numbers of fleas. For example, an immature female that weighed only 225 grams in August, when the average weight for that age and sex was between 350 and 400 grams, was found to be harboring 276 fleas. However, an adult female which proved to be suffering from the pneumonic form of tularemia had only 10 fleas. Three immature squirrels, also infected with tularemia, had 33, 50, and 180 fleas respectively. Many of the extremely high counts, exceeding 100 fleas per animal, were obtained from apparently healthy normal squirrels. There was no indication that the flea count of a squirrel was related to its health.

Since each squirrel was given a distinctive identification mark, it was possible to keep track of the numbers of fleas taken from individual hosts. Such case histories indicated considerable fluctuations from day to day and gave some suggestion of the rate of re-infestation. During each flea-sampling period, all fleas were removed each time a squirrel was captured, but this did not seem to affect consistently the number of fleas present at succeeding captures, as illustrated by the following squirrel history, that of an immature male:

Date of capture	No. of fleas	Date of capture	No. of fleas
1942		1942	
June 26	22	30	22
July 10	35	November 1	28
13	21	20	115

14	7	21	130
28	55	22	42
29	47	23	42
30	28	25	31
August 6	27		
7	39	1943	
8	28	January 6	131
12	20	7	177
21	21	8	147
September 15	20	9	85
29	64	February 3	28
October 1 (a.m.)	13	March 16	38
1 (p.m.)	10		111
2	93		61
27	24	April 29	13
28	30	May 1	17

In the above illustration, 1835 fleas were taken in 37 collections from a single squirrel over a ten-month period. It is evident that squirrels may be readily re-infested with fleas within very short periods of time. This phenomenon had been demonstrated some years prior to the present study by rodent investigations in the Sierra Nevada (Meyer 1938). Since these fleas normally leave their hosts for varying lengths of time, it is possible that this degree of re-infestation is a fair measure of the natural rate of flea movements. If this is so, the exposure of an individual squirrel to such a large number of parasites in a limited time must be a factor of considerable importance in the epidemiology of flea-borne ground squirrel infections.

The variations in flea counts revealed by repeated

observations of the same and of different squirrels probably reflect variations in the flea populations inhabiting the squirrel nests. We did not excavate any nests which were in active use by the squirrels, for we wanted to keep conditions in the community as natural as possible. However, the preliminary survey of 1940 provided a comparison of the numbers of fleas on squirrels with those in the entrances of squirrel burrows (Stewart and Evans 1941). Flea counts from burrow entrances were much lower than those from the squirrels; they generally averaged less than 4 per entrance, and the largest number recorded from a single burrow entrance was 107, taken July 14, 1942. However, these entrance samples correlated well with those from the squirrels, for they showed a similar predominance of both *H. anomalous* and *D. montanus* and a similar seasonal shift in the relative abundance of these two species. Since these fleas are known to breed in the squirrel nests which are situated underground, changes in the subterranean environment may be the controlling factor influencing the development of the flea populations. Although microclimatic conditions in the burrows tend to be more uniform than those above ground and thus probably provide a more favorable breeding habitat for the fleas, little is known of the variations in microclimate existing there. The position of the squirrel nest in relation to the ground surface is important in this connection; some nests have been found only six inches below the surface, where temperature and humidity are probably more variable than in nests at greater depths. The age and status of the burrow system should also be considered, for old systems and nests sometimes contain large amounts of decaying fees and nest material that may be favorable to flea development, while newly constructed nests would harbor few adult fleas for some days. An investigation of the breeding habitat is

necessary to further understanding of the growth of flea populations.

TICKS

Tick collecting was relatively limited in 1940, when only 29 were secured from squirrels. In 1941, approximately thirty squirrels per month were examined for ticks from April through November (except for July), and 121 ticks were taken. In 1942 similar examinations were made in late March, late May and at intervals from July 6 to November 30, in which time 629 squirrel examinations were made and 2432 ticks obtained. In 1943, collecting was accomplished in every month except November; 598 squirrel examinations were made and 979 ticks taken. Less extensive work was undertaken in 1944, but from February through August 567 ticks were secured from 305 squirrel examinations. A total of 977 ticks were taken from 284 squirrels in the period from March through July and in November, 1945.

In the first two years of the study not all of the ticks were identified, but from 1942 on all specimens were determined at least to genus. Three genera, *Dermacentor*, *Ixodes* and *Haemaphysalis*, were encountered on the squirrels, represented by the following species: *D. occidentalis*, *I. pacificus*, *I. sculptus* and *H. leporis-palustris*. The one record of the latter appeared to be a case of accidental parasitism; *I. sculptus* proved to be host specific for ground squirrels in this area, while *I. pacificus* and *D. occidentalis* occurred on many other hosts. *Ornithodoros turicata* was found in all stages of development in the squirrel burrows but never on a host animal; this species was obtained by scraping out the burrow as far back as three feet from the entrance and sifting the scratchings from the bottom of the burrow where it was slightly moist.

Figures showing the percentage of squirrels infested with ticks of all species (Fig. 6) and the num-

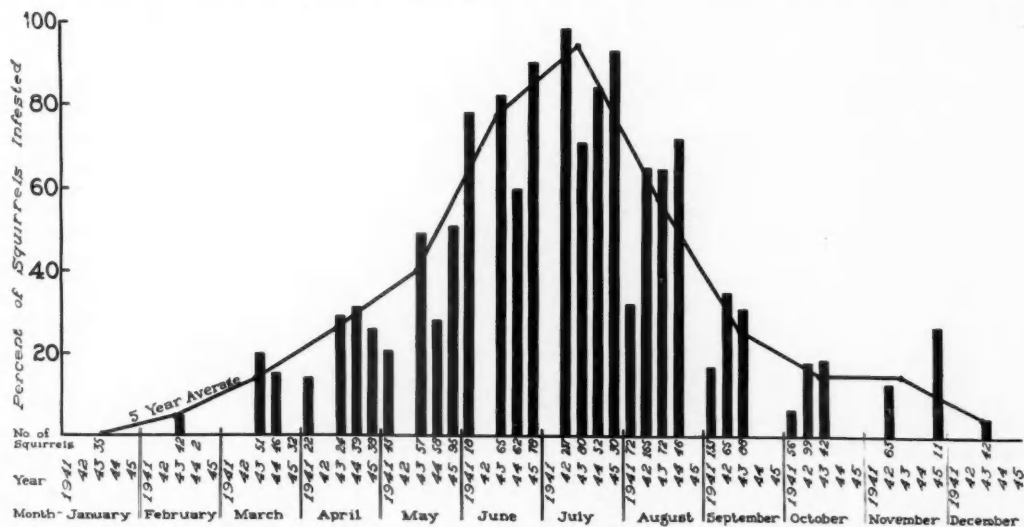


FIG. 6. Percentage of squirrels infested with ticks in each month of the investigation, Calaveras Dam, 1941-45.

bers of ticks found per every 10 hosts (Fig. 7) indicate a marked seasonal occurrence of these ectoparasites on the squirrels. Very few were encountered in the winter months, and it was not until March that they began to be taken with appreciable frequency. The degree of infestation then rose steadily and reached its peak in mid-summer, generally July, when from 82 to 98% of the squirrels had ticks. From this peak point, decline was equally steady and by November not more than 20% were ever infested. This tick "season" clearly reflects the rhythmic life history cycle of these arthropods. It suggests that tick-borne diseases may run a rather different epizootic course from that of diseases carried by fleas.

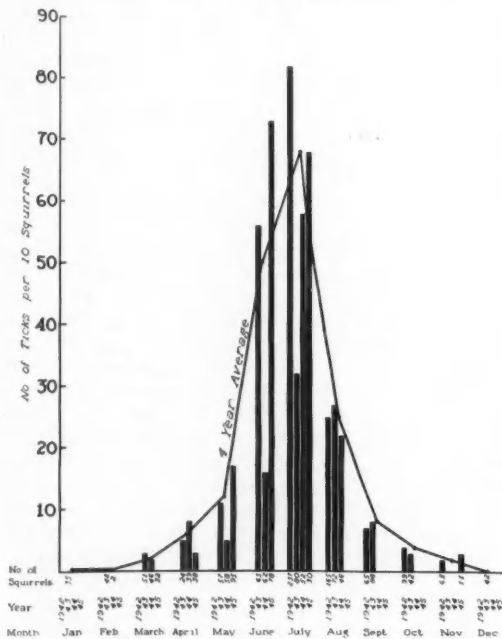


FIG. 7. Numbers of ticks per every 10 squirrels in each month of the investigation, Calaveras Dam, 1942-45.

During the peak of the tick season there seemed to be a continual supply of hungry ticks waiting for suitable hosts, to which they usually attached on the head, neck, shoulder, under the foreleg, or occasionally on a foot or near the anus. Although as many as 67 ticks were sometimes taken from a single squirrel, the number per host was usually much smaller, most frequently less than six (Table 1). Even at the height of the tick season, when nearly all of the squirrels were infested, the maximum average number of ticks per squirrel was only 8.2. This is in contrast to the large numbers sometimes occurring on other host species; in Minnesota the varying hare (*Lepus americanus*) has been found to harbor as many as 16,000 ticks (*Haemaphysalis leporis-palustris*) on a single hare and in some months to average as many as 4000 ticks per host (Green, Evans, and Larson 1943). It has been suggested that in years of heavy

infestation all of the tick-feeding space on the hare is occupied (Green, Evans, Bell, Larson, and Mather 1937). No such extreme utilization of the host was found with the Calaveras Dam ground squirrels.

TABLE 1. Tick collection from California ground squirrels by month and the degree of infestation per squirrel, Calaveras Dam, 1942-45.

Month	Number of squirrels examined	Number of ticks taken	PERCENT OF SQUIRRELS INFESTED WITH TICKS					
			Number of ticks					
			0	1-5	6-10	11-15	16-20	over 20
January	35	0	100					
February	44	2	96	4				
March	129	22	85	14				
April	101	59	71	26	3	1		
May	210	258	56	38	5			
June	205	1022	22	50	15	7	4	2
July	399	2697	6	48	27	12	3	4
August	283	706	35	54	8	0	0	1
September	153	116	67	31	1	1		
October	141	55	82	17	1			
November	74	16	85	15				
December	42	2	95	5				
Total	1816	4955						

Laboratory studies have shown that various animals, when first infested with large numbers of larval ticks, acquire a resistance which prevents subsequent batches of larvae from engorging on them (Trager 1939, Gregson 1942). There was no evidence of such acquired resistance among the ground squirrels at Calaveras Dam. Comparison of the number of ticks found on young and adult squirrels failed to show any significant difference, as illustrated by the following figures for July 1942:

No. of ticks per squirrel	Per cent of squirrels infested	
	Young	Adults
0	1	6
1-5	42	38
6-10	30	30
11-15	13	22
16-20	6	0
over 20	8	4

It is possible that some resistance may have been acquired by the young squirrels before they left their nests after the weaning period.

Like fleas, the ticks showed considerable ability to re-infest hosts from whom these ectoparasites had been removed. Squirrels often regained as many or more ticks within a day or so of being de-ticked:

Date of capture	No. of Ticks
Squirrel No. 1	
July 16	23
17	23
24	19
Squirrel No. 2	
July 6	8
8	22
10	20

The rate of re-infestation was at times quite rapid. Some squirrels were examined at intervals of less

than one half-day, and their ticks removed at each capture. These individuals sometimes acquired more ticks within a few hours, as indicated by the following examples:

Date of capture	No. of ticks	
	A.M.	P.M.
July 22	4	8
July 30	4	7
October 1	3	1

Data on the occurrence of the different tick species are presented in Table 2. *Dermacentor occidentalis* appeared to be the most abundant species on the squirrels and occurred in greater numbers than any other tick. It was taken most frequently in June and July, but practically disappeared from these hosts in September. Nymphs were taken much more frequently than larvae, even at the beginning of the tick season when the earlier life stage forms must actually have been present in greater numbers. In the laboratory, larvae completely engorged in from 3 to 5 days, while nymphs required from 5 to 8 days; thus nymphs, by remaining on the host about twice as long as larvae, had about twice the chance of being collected. Size of host also has a bearing on the life stage collected; adults were not found on any rodents and were taken only from larger hosts such as raccoon (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), and black-tailed deer (*Odocoileus hemionus*), while larvae were much more abundant than nymphs on the smaller rodents such as the deer-mouse (*Peromyscus maniculatus*). Similar distribution of nymphs and larvae of *D. occidentalis* has been found to occur elsewhere (Kohls 1937). The need for intermediate hosts makes this tick, and others with similar requirements, particularly significant as a potential agent of disease transfer.

Ixodes sculptus was the second most abundant tick on ground squirrels. This species infested squirrels most heavily from April through August but continued to be taken in small numbers in all the winter months except January. Nymphs comprised 68% of the total and were collected from March through December, while larvae, representing only 2%, were taken from May to September. The remaining 30% of the 864 *I. sculptus* taken from ground squirrels were adults. With the exception of a single male, which was not attached for feeding, all adults found on the squirrels were females; three additional males were found in squirrel burrows. Nuttall (1911) pointed out that adult male ticks of species that parasitize hosts with a more or less fixed habitat are rarely found on the hosts and that mating of these ectoparasites takes place in the host's nest. At the Calaveras Dam, this species was recorded only from *Citellus beecheyi*, except for single specimens found on a gray fox and a spotted skunk (*Spilogale gracilis*) respectively.

Ixodes pacificus was taken on squirrels much less frequently than either of the two species just discussed, and their occurrence on these hosts was apparently limited to the months from March through July. Only 42 specimens were collected from squir-

TABLE 2. Monthly averages by species of the number of ticks per every 10 California ground squirrels, Calaveras Dam, 1942-44.

Month and year	<i>I. sculptus</i>	<i>I. pacificus</i>	<i>D. occidentalis</i>	Total
January				
1943....	0	0	0	0
February				
1943....	*	0	..	*
1944....	0	0	0	0
March				
1943....	2	1	0	3
1944....	1	1	0	2
April				
1943....	2	1	3	6
1944....	7	*	0	7
May				
1943....	1	1	8	10
1944....	1	*	1	3
June				
1943....	15	3	36	54
1944....	6	*	10	16
July				
1942....	18	0	63	81
1943....	(no ticks were identified this month)			32
1944....	6	1	48	55
August				
1942....	15	0	15	30
1943....	14	0	13	27
1944....	12	0	12	24
September				
1942....	9	0	1	10
1943....	6	0	1	7
October				
1942....	1	0	0	1
1943....	2	0	0	2
November				
1942....	*	0	0	*
December				
1943....	*	0	0	*

*Indicates that the species was present but in numbers of less than one tick per 10 squirrels.

rels, but they were also found on a wide variety of other hosts, including several species each of birds and lizards. Adult *I. pacificus* were not taken on ground squirrels but, like those of *D. occidentalis*, were restricted to larger hosts such as deer, horse, and dog.

LICE

Sucking lice, *Neohaematopinus laevisculus*, were found on the squirrels throughout the year. They were most abundant on young squirrels just out of the nest. Although as many as 300 were found on a single host, they were most frequently present in numbers of less than 100. *Enderleinellus osborni* was collected only once, in July 1945, but because of its small size it may have been previously overlooked. Both of these species of louse are common parasites of *Citellus beecheyi* and other kinds of ground squirrels.

HEMIPTERA

A single cone-nosed bug, *Triatoma protracta*, was found in a trap with a squirrel in the summer of 1940. This species was also taken several times in association with desert and dusky-footed wood rats. It is possibly of epidemiological significance, because

it is known to transmit the trypanosomes of Chagas' disease.

THE ROLE OF GROUND SQUIRRELS IN COMMUNITY HOST-PARASITE RELATIONSHIPS

This population of California ground squirrels and their burrows yielded a total of sixteen ectoparasite species, including two sucking lice, one cone-nosed bug, eight fleas, and five ticks. These were separable into four main groups on the basis of their host occurrence. The first group includes those which were either entirely restricted to *C. beecheyi* or found singly on one or two other hosts:

Neohaematopinus laevisculus
Enderleinellus osborni
Ixodes sculptus
Ornithodoros turicata

A second group was formed by species also largely specific for ground squirrels but taken occasionally on a good many other hosts:

Diamanus montanus
Hoplopsyllus anomalus

Group three was made up of those species which did not seem especially characteristic of *Citellus* and which occurred as frequently on a wide variety of other hosts:

Dermacentor occidentalis
Ixodes pacificus

The fourth and largest group was comprised of those ectoparasites which were only accidentally or casually associated with ground squirrels and which were more frequently taken from other hosts:

Triatoma protracta
Atyphloceras multidentatus
Monopsyllus wagneri
Opisodasys nesiotus
Orchopeas sexdentatus
Anomiopsyllus falsicalifornicus
Pulex irritans
Haemophysalis leporis-palustris

Twenty species of mammals which were natural members of the community were brought into the relationship of having one or more of these ectoparasites in common with the ground squirrel. Thus included were all of the mammal species examined, except the bats, shrews, and the pocket gopher (*Thomomys bottae*). To this list may be added man, dog, and horse, three species of birds and three of lizards. It is of some interest to consider briefly the organization of the mammalian community from the standpoint of the ground squirrels and to examine the channels by which ectoparasites might be transferred from one host species to another.

A number of the smaller mammals, when released after capture, frequently disappeared into the ground squirrel burrows. Grass cuttings left by the meadow vole (*Microtus californicus*) were found a number of

times at the mouths of squirrel burrows, where the voles apparently felt sheltered and could consume their food with more leisure. It seems probable that the pocket mouse (*Perognathus californicus*), harvest mouse (*Reithrodontomys megalotis*), and the various species of *Peromyscus* (*P. maniculatus*, *P. truei*, and *P. californicus*) also made use of the burrows as temporary or permanent shelters. Squirrel trails through both green and dry vegetation were used by all of these rodents. Among these common denizens of the burrows and trails, parasite transfer could be effected directly from host to host or, more commonly, indirectly from nest material, burrow walls and entrances, and the trail surfaces, where the parasites are left by one individual to be picked up subsequently by another. The ground squirrels seemed to be particularly effective in seeding their habitat with parasites, especially with fleas, with which other animals might come in contact. The evidence suggested that passage from ground squirrels to smaller mammals occurred more frequently than passage in the opposite direction.

Predation on the ground squirrels is also a factor permitting transfer of parasites from prey to predator. Mammals of the area which may be classified as actual or potential predators include the long-tailed weasel (*Mustela frenata*), gray fox, coyote (*Canis latrans*), raccoon, badger (*Taxidea taxus*), and bobcat (*Lynx rufus*). Such cases of transfer are often examples of accidental parasitism but may also include instances of normal progress from intermediate to final host.

A related but distinct category seemed to apply to other mammals such as the opossum (*Didelphis virginiana*), the striped skunk (*Mephitis mephitis*), and the spotted skunk, which frequently excavated the ground squirrel burrows. Their purpose in doing so did not seem to be to molest the squirrels themselves, but rather to search for smaller prey or often to enlarge the burrows for their own use.

The activity of the squirrels above ground carried them into habitats occupied by a number of other mammals and provided further possibility for contact between species. In rocky piles they were often associated with desert woodrats (*Neotoma lepida*), deer-mice (*Peromyscus maniculatus*), and piñon-mice (*Peromyscus truei*), in areas of brush and trees with dusky-footed woodrats (*Neotoma fuscipes*), gray squirrels (*Sciurus griseus*), chaparral-mice (*Peromyscus californicus*), and brush rabbits (*Sylvilagus bachmani*), and in open grassy places with cottontails (*Sylvilagus audubonii*), jackrabbits (*Lepus californicus*), black-tailed deer, and others of the smaller mammals previously mentioned.

These community host-parasite relationships have been postulated on the basis of ectoparasite species common to the ground squirrel and one or more other mammalian hosts. A similar picture could be developed from the standpoint of each of the other host species. The intricate web of interrelationships that would result from a composite treatment of the community would be too complex for adequate repre-

sentation. Host records for the various ectoparasites are given at length in the Appendix. The distribution of the several host species according to the number of parasite species recorded for each is indicated as follows:

Number of parasite species per mammal host species				
	1-3	4-6	7-9	10-12
Number of mammal host species.....	11	8	6	3
Percentage of total mammal host species.....	39.3	28.6	21.4	10.7

Of the 28 species of free-living, non-domestic mammals examined, 17 had from four to twelve species of ectoparasites. Six host species yielded only one kind of ectoparasite in each case, but this was probably due to the infrequency of examination rather than to actual freedom from parasitism. During the period of this investigation no conditions were observed which might have led to an unusual concentration of ectoparasites, and there is no reason to believe that this degree of parasitism is not shared by other mammal faunas of similar structure.

In such a parasitological survey, the extent of specificity of host selection is of considerable interest. The distribution of the several parasite species according to the number of mammalian host species recorded for each is shown as follows:

Number of mammal host species per parasite species				
	1-3	4-6	7-9	10-12 13-15
Number of parasite species.....	51	5	3	1 1
Percentage of total parasite species from mammal hosts.....	83.7	8.2	4.9	1.6 1.6

Of the 65 ectoparasite species with definite mammal host records, 40 were taken from single host species. As suggested above, the infrequency with which some of the hosts were examined may account for some of this apparently high degree of host specificity. Nevertheless, 17 species of ectoparasites were almost certainly host-specific in the Calaveras Dam area, as follows:

<i>Trichodectes octomaculatus</i>	<i>Hoplopleura acanthopus</i>
<i>Trichodectes mustelae</i>	<i>Hoplopleura sciuricola</i>
<i>Trichodectes quadraticeps</i>	<i>Solenopotes ferrisi</i>
<i>Geomydoecus geomydis</i>	<i>Cimex pilosella</i>
<i>Neohaematopinus laevisculus</i>	<i>Lipoptena depressa</i>
<i>Neohaematopinus neotomae</i>	<i>Trichobius corynorhini</i>
<i>Fahrenheitia tribulosa</i>	<i>Myodopsylla gentilis</i>
<i>Enderleinellus osborni</i>	<i>Ixodes sculptus</i>
<i>Polyplax abscisa</i>	

Thirteen species were probably restricted to small groups of closely related host species, as for example the louse *Trichodectes mephitis* found on both striped and spotted skunks. Others in this category include the following:

<i>Haemodipsus</i> sp. nov.	<i>Odontopsylla dentatus</i>
<i>Polyplax auricularis</i>	<i>Cediopsylla inaequalis</i>
<i>Hoplopleura hesperomydis</i>	<i>Ornithodoros</i> sp. undet.
<i>Linognathus setosus</i>	<i>Ixodes jellisoni</i>
<i>Fozella ignota</i>	<i>Spinecturnix</i> sp. undet.
<i>Histrichopsylla gigas</i>	<i>Notoedres cati</i>

From the standpoint of disease transfer, the ectoparasites with the least host specificity would seem to be of greatest significance. Six fleas (*P. irritans*, *H. anomalus*, *D. montanus*, *M. telchinum*, *O. sex-dentatus*, *O. nesiotus*) and two ticks (*D. occidentalis*, *I. pacificus*) were the most widely dispersed species, being found on from 6 to 17 different species of hosts. All of these ectoparasites have been found naturally infected with, or have been experimentally proved capable of transmitting, such disease organisms as those of plague and tularemia. All of these species were taken by us from ground squirrels, which thus appeared to be unusually exposed to the possibility of arthropod-borne infection.

ECTOPARASITES ENCOUNTERED ON MAN

Field workers on this project were subject to occasional infestation by the various species of ectoparasites. Only five species were actually encountered on the men or their clothing. *Pulex irritans* was taken at almost every summer examination of deer beds, where this species was present in large numbers. The fleas quickly crawled up trouser legs and many attempted to obtain blood meals immediately; as many as 60 fleas were removed from one man after less than a minute's contact with the beds. *Hoplopyllus anomalus* was also found on bodies or clothes on several occasions and was twice noted as drawing blood. The other abundant squirrel flea, *Diamanus montanus*, did not appear to infest man. In August 1944, after probing a squirrel burrow by hand, one worker found several larval *Ornithodoros turicata* on his arm; some of them were already partially engorged by the time they were detected. *Derma-centor occidentalis* was collected from man rather frequently; adults were taken in February, March, May, June, July and November, and immatures in June and July. *Ixodes pacificus* was recorded twice from workers, an adult female in April and a nymph in June. All of these records were accidental and, considering the magnitude of the project, surprisingly few. Nevertheless, it is by such accidents as these that the causative agents of many diseases are transmitted from their natural host reservoirs to human populations where, once established, they may break out in epidemic form.

ECTOPARASITE-TRANSMITTED DISEASES

PLAGUE

In November 1933 a ground squirrel shot at the Calaveras Dam by the California State Department of Public Health proved to be plague-infected. Subsequent routine surveys failed to show further evidence of this disease organism (*Pasteurella pestis*) in this area until the summer of 1942, when it was again isolated from squirrel organs and fleas (Meyer, Holdenried, Burroughs, & Jawetz 1943). Although during the six years of our study there was no indication of epizootic plague, it was evidently latent within the community.

Both of the squirrel fleas, *D. montanus* and *H. anomalus*, were also found plague-infected at the

Calaveras Dam in the summer of 1942 (Meyer, et al. 1943). No plague-infected ticks were found in our study area, but the State Department of Public Health reported 13 pools of infected ticks from ground squirrels, jack rabbits and cottontails in California from 1941 through 1943. In view of the large number of host species parasitized by some ticks and the fact that individual ticks may require several different hosts, the extent to which ticks are involved in the transmission of plague should be investigated.

Routine laboratory testing of the organs of other rodent species was initiated in 1943, but none was found positive for plague. Most of these rodents have been proved naturally plague-infected at various times elsewhere in California. Recent observations (Meyer and Holdenried 1949) indicate that plague may be spread from wild to domestic rodents; on a ranch where plague infection was demonstrated in both ground squirrels and rats (*Rattus norvegicus* and *R. rattus*), infected squirrel fleas, *D. montanus* and *H. anomalus*, were obtained from rats, while rat fleas, *Nosopsyllus fasciatus* and *Leptopsylla segnis*, were entirely absent from ground squirrels.

TULAREMIA

In 1943 and 1944, tularemia (*Pasteurella tularensis*) was isolated from the organs of six ground squirrels, two pools of ticks removed from ground squirrels, the organs of two meadow voles, and a pool of fleas from the meadow voles, all collected at the Calaveras Dam. No tularemia epizootic was observed on the study area in the six years covered by this investigation. Although an estimated 93,000 ectoparasites were inoculated into guinea pigs, *P. tularensis* was detected only 10 times. Like plague, tularemia appeared to be in enzootic form among the ground squirrels during this study. Evidence that fleas may not play an important part in the spread of this disease has been reported in a study of a tularemia epizootic near San Francisco (Burroughs, Holdenried, Longanecker, & Meyer 1945). Ticks are generally considered to be the most important vectors. The tularemia-infected ticks from the Calaveras Dam were not identified, but the following species found there have been reported naturally infected: *Haemaphysalis leporis-palustris* by Parker & Spencer (1927), *Dermacentor occidentalis* by Parker, Brooks, & Marsh (1929), and *Ixodes pacificus* by Davis & Kohls (1937).

TRYPANOSOMIASIS

Several young squirrels, brought to the laboratory in July and August 1940, lost weight while they were held under observation. They showed a marked anemia, and blood films revealed trypanosomes, approximately one in every twenty fields. Mrs. B. S. Davis in the Zoology Department of the University of California at Berkeley has kindly determined that they resemble *Trypanosoma otospermophili* (Wellman & Wherry) and are in the *lewisi* group of trypanosomes rather than the *cruxi* group as originally stated by Meyer et al. (1943). The life history of this species has not been studied, but other species in the group

pass through a development cycle in fleas, passing out with the feces in the infective stage. One or both of the squirrel fleas, *D. montanus* and *H. anomalus*, probably serve as intermediate hosts and vectors for the trypanosomes.

RELAPSING FEVER

The spirochetes of relapsing fever, *Borrelia turicatae* (Brumpt), were recovered from three of five pools of *Ornithodoros turicata* which had been collected from squirrel burrows (Burroughs & Holdenried 1944). This tick has been reared in the laboratory for five generations with relapsing fever spirochetes passing from generation to generation by ovarian transmission (Davis 1943). Pavlovsky & Skrynnik (1945) report that naturally infected females of *Ornithodoros papillipes*, kept in the laboratory for as long as 13 years, have been able to transmit relapsing fever spirochetes to guinea pigs throughout that time. If this occurs in nature, the tick vector may be a more efficient spirochetal reservoir than the mammalian host.

SUMMARY

A field study of the California ground squirrel and associated mammals in a natural community at the Calaveras Reservoir and Dam in Alameda and Santa Clara Counties, California, from 1940 to 1945 included the collection and identification of approximately 72,000 ectoparasites, and the inoculation of many of them into laboratory test animals for the detection of disease organisms. The 65 species of ectoparasites, taken from one or more of the 28 mammalian host species, included 22 species of fleas, 12 of sucking lice, 5 of biting lice, 2 of flies, 2 of true bugs, 13 of ticks and 9 of mites. Particular emphasis was placed on the fleas and ticks of the ground squirrels.

The flea population from ground squirrels consisted almost entirely of two species, *Diamanus montanus* and *Hoplopsyllus anomalus*. The latter was most abundant and predominated in the flea fauna during the summer months, the former from October through March. A combined index of flea density indicated a low density in late spring, when the young squirrels are born and confined to their burrows, and a high density throughout the winter and until the time of increased squirrel activity and the mating period in early spring. Squirrels were often quite heavily re-infested with fleas soon after their previous ectoparasites had been removed. Male squirrels harbored a greater number of fleas than females.

The ground squirrel tick population showed a marked seasonal fluctuation, reflecting the development of the ticks; they occurred in greatest numbers during the summer, and only a few squirrels were found infested in the winter months. Like the fleas, the ticks readily re-infested squirrels previously relieved of ectoparasites. Both adult and immature *Ixodes sculpus* occurred on the squirrels, but only nymphs and larvae of *I. pacificus* and *Dermacentor occidentalis*. The seasonal occurrence of ticks suggests that tick-borne diseases run a rather different course from that of flea-borne infections.

The various ectoparasites collected from ground squirrels showed differing degrees of host specificity. Twenty other mammals had one or more ectoparasites in common with the ground squirrel. Some of these mammals apparently occupied the ground squirrel burrows, some were actual or potential predators of the squirrels or of the other mammals living with them, and some were associated with the ground squirrels because they occupied habitats entered by the latter during their daily activities. These various relationships illustrate the means by which ectoparasites may be transferred from one host to another and the extent to which the mammalian community may be linked together by parasitism.

Five species of ectoparasites were encountered at various times on the field workers engaged in this study. These accidental occurrences demonstrate the manner in which man may acquire ectoparasite-borne diseases.

Plague, tularemia, trypanosomiasis, and relapsing fever were isolated from the mammal hosts or their ectoparasites. No epizootics were observed in the area, and both plague and tularemia were evidently latent during the period of this study.

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APPENDIX

Annotated Ectoparasite-Host List from Calaveras Dam, Alameda Co., California

(Initials in parentheses indicate name of determiner, given in full in the Introduction.)

Class INSECTA

Order MALLOPHAGA

Family Trichodeetidae

Trichodectes octomaculatus Paine

Host: Raccoon, *Procyon lotor*

Date: July 23, 1940—several. (O. C.).

Trichodectes mustelae Schrank

Host: Long-tailed weasel, *Mustela frenata*

Date: May 6, 1941—several. (O. C.).

Trichodectes mephitis Packard

Host: Striped skunk, *Mephitis mephitis*

Date: June 16, 1940—several. (O. C.).

Host: Spotted skunk, *Spilogale gracilis*

Date: July 23, 1944—several. (W. L. J.).

Trichodectes quadraticeps Chapman

Host: Gray fox, *Urocyon cinereoargenteus*

Date: May 21 and 25, 1941—several thousand from each of three pups examined; also taken in large numbers from an adult. (O. C.).

Geomys geomydis (Osborn)Host: Pocket gopher, *Thomomys bottae*

Date: March 16, 1943—moderate numbers on 1 individual (W. L. J.).

April 4, 1945—well over 100 on a gopher. (R. H.).

Family Menoponidae

Myrsidea latifrons (Carriker)Host: Nests of cliff swallow, *Petrochelidon pyrrhonota*

Date: July 20, 1945—several. (K. E. M.).

Order ANOPLURA

Family Haematoplinidae

Neohaematopinus laeviusculus (Grube)Host: California ground squirrel, *Citellus beecheyi*

Date: Present throughout the year. Most frequently found on young squirrels. June 4, 1941; June 14, 1941 (O. C.); Dec. 20, 1943; June 8, 1944 (W. L. J.).

Neohaematopinus neotomae FerrisHost: Dusky-footed woodrat, *Neotoma fuscipes*

Date: August 20, 1942—1. (W. L. J.). A number of other wood rats were examined, but this louse was obtained only once.

Fahrenholzia tribulosa FerrisHost: California pocket mouse, *Perognathus californicus*

Date: November 13 and 19, 1941. (One mouse harbored over 100 lice.) Obtained on three different mice. (O. C.).

Enderleinellus osborni K. & F.Host: California ground squirrel, *Citellus beecheyi*

Date: July 10, 1945—5. (W. L. J.).

Polyplax auricularis KelloggHost: Chaparral mouse, *Peromyscus californicus*

Date: September, 1943 (day not recorded). (W. L. J.).

Polyplax abscisa FahrenholzHost: California meadow vole, *Microtus californicus*

Date: Nov. 12, 1941—10. (W. L. J.); March 22, 1945. (D. P. F.).

Hoplopleura acanthopus (Burmeister)Host: California meadow vole, *Microtus californicus*Date: March 22, 1945—7. (W. L. J.). Either this species or *P. abscisa* or both present throughout the year. Recorded as early as March and as late as November. Heavy infestations, up to several hundred, on some mice, particularly old males. Young hairless mice found in nests also had lice.*Hoplopleura hesperomydis* (Osborn)Host: Deer-mouse, *Peromyscus maniculatus*

Date: April 13, 1945—3. (W. L. J.).

Hoplopleura sciuricola FerrisHost: Western gray squirrel, *Sciurus griseus*

Date: July 10, 1945—6. (W. L. J.).

Linognathus setosus (Olfers)Host: Brush rabbit, *Sylvilagus bachmani*

Date: May 10, 1944—1. (W. L. J.).

Solenopotes ferrisi (Fahrenholz)Host: Black-tailed deer, *Odocoileus hemionus*

Date: October 6, 1943—50 collected; more were present. (W. L. J.).

Haemodipsus sp. nov.Host: Brush rabbit, *Sylvilagus bachmani*

Date: May 10, 1944—1. (W. L. J.).

Host: Cottontail, *Sylvilagus audubonii*

Date: March 22, 1945—5; July 12, 1945—11. (W. L. J.).

Order HEMIPTERA

Family Reduviidae

Triatoma protracta (Uhler)

Host: Taken in trap with California ground squirrel,

Citellus beecheyi

Date: Summer, 1940—1. (R. L. U.).

Host: Taken in traps with desert woodrat, *Neotoma lepida*.

Date: Summer, 1940—several. (S. F. W.).

Resting place: Found only in one or two of about 8 dusky-footed woodrat houses (*Neotoma fuscipes*).

Date: Spring, 1941—several. (R. H.).

Family Cimicidae

Cimex pilosellus (Horvath)Host: Yuma bat, *Myotis yumanensis*.

Date: June 13, 1943—9 collected from 8 adult and 32 immature bats which left their roost beneath a tile roof in the unusually hot afternoon. May 8, 1944—obtained again from bats flying at night. November 30, 1944—11 collected at a roost of this host. (R. L. U.).

Oeciacus vicarius HorvathHost: Cliff swallow, *Petrochelidon pyrrhonota*.

Date: July 19 and 20, 1945—over 100 bed bugs in some nests. (R. L. U.).

Order DIPTERA

Family Hippoboscidae

Lipoptena depressa (Say)Host: Black-tailed deer, *Odocoileus hemionus*.

Date: October 6, 1943—about 30. June 2, 1945—12 from a dead fawn. (W. L. J.).

Family Streblidae

Trichobius corynorhini CockerellHost: Long-eared bat, *Corynorhinus rafinesquii*.

Date: March 15, 1945—2 (R. L. W.).

Order SIPHONAPTERA

(Families according to Jellison and Good, 1942)

Family Ischnopsyllidae

Myodopsylla gentilis Jordan and RothschildHost: Yuma bat, *Myotis yumanensis*

Date: June 16, Aug. 10, 1943; September 28 and 30, 1943—several; Aug. 26, 1944—28; Aug. 24, 1944—20. (P. Q. T.).

Eptescopysylla vancouverensis (Wagner)Host: Long-eared bat, *Corynorhinus rafinesquii*

Date: March 10, 1946—2 ♀ ♀. (P. Q. T.).

Family Hystrichopsyllidae

Athyphloceras multidentatus (Fox)Host: Burrow of California ground squirrel, *Citellus beecheyi*

Date: April 29, 1940—1 ♂. (M. A. S.).

Hystrichopsylla gigas (Kirby)Host: California meadow vole, *Microtus californicus*

Date: March 22, 1945—3. (A. L. B.).

Peromyscopsylla hemispherum StewartHost: California pocket mouse, *Perognathus californicus*

Date: December 9, 1940—1 ♀. (R. T.).

Host: Chaparral mouse, *Peromyscus californicus*

Date: October 24, 25, 26 and 29, 1941—10 from 4 mice. (R. T.).

Host: Deer-mouse, *Peromyscus maniculatus*, and piñon mouse, *P. truei*.

- Date: Taken on occasion from both species, usually in the fall. (R. T.).
- Carteretta carteri* Fox
Host: California pocket mouse, *Perognathus californicus*
Date: Taken in May, June, September, October and November. Of 32 pocket mice examined, 13 were flea-infested, 12 of them with *C. carteri*. Never more than one or two on one host. (W. L. J.).
Host: Deer-mouse, *Peromyscus maniculatus*.
Date: December 5, 1940—1 ♂. (W. L. J.); April 3, 1942—2. (A. L. B.).
- Merigis cummingsi* (Fox)
Host: California meadow vole, *Microtus californicus*
Date: July 8, 1944—1. (F. M. P.).
- Ceratophyllus petrochelidoni* Wagner
Resting place: Nests of cliff swallow, *Petrochelidon pyrrhonota*
Date: July 19 and 20, 1945—13 ♂♂ and 18 ♀♀. (G. P. H.).
Dr. Holland in a recent publication (1949) states "*C. petrochelidoni* appears to be rare. The writer has examined many nests of cliff swallows (which are almost undoubtedly the true hosts) for further specimens, but without success. There are no additional Canadian records at this time. Recently Mr. P. Quentin Tomich of the University of California at Berkeley submitted a series of fleas from Calaveras Dam, Alameda Co., California, ex nests of *Petrochelidon albifrons*. These proved to be *Ceratophyllus petrochelidoni*, ———."
- Dasypsyllus gallinulae* (Dale)
Host: Cottontail, *Sylvilagus audubonii*
Date: June 10, 1944—1. (G. P. H.).
- Diamanus montanus* (Baker)
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 21, 1941—1 ♂, 2 ♀♀; May 28, 1941—1 ♀. (W. L. J.) July 31, 1944—1. (A. L. B.).
Host: California ground squirrel, *Citellus beecheyi*
Date: Taken in variable abundance throughout the year on hosts and in their burrows. (M. A. S., W. L. J., and R. H.).
Host: California pocket mouse, *Perognathus californicus*
Date: May 9, 1940—1 ♂ (W. L. J.).
Host: Desert woodrat, *Neotoma lepida*
Date: November 12, 1940—1 ♀. (W. L. J.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: May 3, 1940—1 ♂. (W. L. J.).
Host: Cottontail, *Sylvilagus audubonii*
Date: June 16, 1943—1; May 8, 1944—1. (A. L. B.).
- Fozella ignota* (Baker)
Host: Long-tailed weasel, *Mustela frenata*
Date: May 6, 1941—3 ♂♂, 4 ♀♀; June 9, 1941—1 ♂. (W. L. J.).
- Malareus telchinum* (Roths.)
Host: Western harvest mouse, *Reithrodontomys megalotis*
Date: November 14, 1941—1; July 9, 1943—1. (A. L. B.).
Host: Chaparral mouse, *Peromyscus californicus*
Date: October 29, 1940—3 ♂♂, 3 ♀♀. (W. L. J.).
July 30, 1942—1. (A. L. B.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: October 24, 1940—1 ♀; December 7, 1940—1 ♀; September 16, 1941—1 ♀; September 24, 1941—1 ♂. (W. L. J.); Nov. 19, 1941—1; Nov. 21, 1941; March 1943—4; Dec. 22, 1943—1; March 21, 1944—4. (A. L. B.).
Host: Piñon mouse, *Peromyscus truei*
Date: September 23, 1940—1 ♂; May 1, 1941—1 ♀. (W. L. J.); July 30, 1942—3. (A. L. B.).
Host: Desert woodrat, *Neotoma lepida*
Date: October 27, 1940—1 ♂ (W. L. J.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: May 30, 1940—1 ♀. (W. L. J.).
- Monopsyllus wagneri* (Baker)
Host: California pocket mouse, *Perognathus californicus*
Date: December 9, 1940—1 ♂. (W. L. J.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: December, 1940—1 ♂, 2 ♀♀. (W. L. J.).
Resting place: Burrow of ground squirrel, *Citellus beecheyi*
Date: July 1, 1940—1 ♂. (M. A. S.).
- Odontopsyllus dentatus* (Baker)
Host: Cottontail, *Sylvilagus audubonii*
Date: May 8, 1944—1. (A. L. B.).
- Opisodasys nesiotus* Augustson
Host: Striped skunk, *Mephitis mephitis*
Date: May 28, 1943—1. (A. L. B.).
Host: California ground squirrel, *Citellus beecheyi*
Date: July 19, 1940—1 ♀; one or two others on various occasions. (M. A. S.).
Host: California pocket mouse, *Perognathus californicus*
Date: September 23, 1940—1 ♀. (W. L. J.).
Host: Western harvest mouse, *Reithrodontomys megalotis*
Date: November 14, 1941—2. (A. L. B.).
Host: Chaparral mouse, *Peromyscus californicus*
Date: October 24, 1940—1 ♀. (W. L. J.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: Taken in every month except January, when no hosts of this species were examined. (W. L. J. and A. L. B.).
Host: Piñon mouse, *Peromyscus truei*
Date: November 13, 1941—2; July 30, 1942—1. (A. L. B.).
Host: Desert woodrat, *Neotoma lepida*
Date: May 6, 1941—1 ♀. (W. L. J.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: July 17, 1942—1; March, 1943—1. (A. L. B.).
Host: California meadow vole, *Microtus californicus*
Date: Nov. 12, 1941—1. (A. L. B.).
- Crochopas sexdentatus* (Baker)
Host: Long-tailed weasel, *Mustela frenata*
Date: May 6, 1941—1 ♀. (W. L. J.).
Host: Spotted skunk, *Spilogale gracilis*
Date: September 30, 1940—1 ♀. (W. L. J.).
Host: California ground squirrel, *Citellus beecheyi*
Date: May 31, 1940—1 ♀; one or two others on several occasions (M. A. S.).
Host: Desert woodrat, *Neotoma lepida*
Date: Taken in every month in which these hosts were examined (May through December). (W. L. J.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: Taken in every month in which these hosts were examined (March through November). (W. L. J. and A. L. B.).
Host: California meadow vole, *Microtus californicus*
Date: May 25, 1941—1 ♀. (W. L. J.).
- Anomiopsyllus falsicalifornicus* Fox
Host: California ground squirrel, *Citellus beecheyi*
Date: July 29, 1944—1. (F. M. P.).

Family Pulicidae

Cediopsylla inaequalis (Baker)

Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 28, 1941—2 ♀♀. (W. L. J.).

Ctenocephalides felis (Bouché)

Host: Opossum, *Didelphis virginiana*
Date: July —, 1942—5. (A. L. B.).
Host: Dog, *Canis familiaris*
Date: Sept. 29, 1943—72 (P. Q. T.).

Hoplopsyllus anomalous (Baker)

Host: Spotted skunk, *Spilogale gracilis*
Date: September 30, 1940—1 ♂, 7 ♀♀; October 2, 1940—2 ♀♀ (W. L. J.); July 23, 1944—6. (A. L. B.).
Host: Striped skunk, *Mephitis mephitis*
Date: May, 1942—1. (A. L. B.).
Host: California ground squirrel, *Citellus beecheyi*
Date: Taken in variable abundance throughout the year on hosts and in their burrows. (M. A. S., W. L. J., and R. H.).
Host: Chaparral mouse, *Peromyscus californicus*
Date: July 30, 1942—1. (A. L. B.).
Host: Dusky-footed woodrat, *Neotoma fuscipes*
Date: August 1, 1942—7. (A. L. B.).
Host: California meadow vole, *Microtus californicus*
Date: June 3, 1941—1 ♀. (W. L. J.); July 22, 1942—2. (A. L. B.).
Host: Cottontail, *Sylvilagus audubonii*
Date: June 16, 1943—2. (A. L. B.).

Hoplopsyllus foxi Ewing

Host: California jackrabbit, *Lepus californicus*
Date: June 17, 1944—1. (A. L. B.).
Host: Cottontail, *Sylvilagus audubonii*
Date: May 8, 1944—2; June 10, 1944—2. (A. L. B.).

Pulex irritans Linnaeus

Host: Opossum, *Didelphis virginiana*
Date: July 24, 1940—1 ♀. (W. L. J.).
Host: Raccoon, *Procyon lotor*
Date: July 23, 1940—2 ♀♀; July 27, 1940—1 ♂, 4 ♀♀. (W. L. J.); July 28, 1944—3. (A. L. B.).
Host: Spotted skunk, *Spilogale gracilis*
Date: September 30, 1940—6 ♂♂, 11 ♀♀; October 2, 1940—12 ♂♂, 15 ♀♀. (W. L. J.); July 23, 1944—7. (A. L. B.).
Host: Striped skunk, *Mephitis mephitis*
Date: June 16, 1940—1 ♀. (W. L. J.).
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 21, 25 and 28, 1941—19 ♂♂, 34 ♀♀; June 21, 1941—1 ♂, 3 ♀♀. (W. L. J.); July 31, 1944—4 ♂♂, 8 ♀♀. (A. L. B.).
Host: California ground squirrel, *Citellus beecheyi*
Date: August 3, 1940—1 ♀; August 22, 1940—1 ♂; single specimens on several occasions in September and October, single specimens also recorded several times from burrows. (M. A. S.).
Host: Desert woodrat, *Neotoma lepida*
Date: May 25, 1941—1 ♀. (W. L. J.).
Host: Black-tailed deer, *Odocoileus hemionus*
Date: June 2, 1945—2. (R. H.); present in deer beds in August, September and October. (A. L. B. and R. H.).

Family Tungidae

Echidnophaga gallinacea (Westwood)

Host: Opossum, *Didelphis virginiana*
Date: June 4, 1941—3 ♀♀. (W. L. J.).
Host: Long-tailed weasel, *Mustela frenata*
Date: June 15, 1944—1. (A. L. B.).

Class ARACHNOIDEA

Order ACARINA

Family Argasidae

Argas reflexus (Fabricius)

Resting place: Roost of bat in an abandoned cabin.
Date: November 30, 1944—6. (R. A. C., part by R. H.).

Argas sp.

Host: California quail, *Lophortyx californicus*
Date: December, 1942—1 larva. (R. A. C.).

Ornithodoros coriaceus Koch

Host: Black-tailed deer, *Odocoileus hemionus*
Date: September 24, 1942—13 larvae; October 6, 1943—14 larvae and nymphs from a dead fawn. Nymphs were also taken on several occasions from April through June 1940 and in June and August 1941 on the ground. (R. A. C. and R. H.).

Ornithodoros turicata (Dugès)

Resting place: Burrow of California ground squirrel, *Citellus beecheyi*
Date: May, July, August and September—adults, nymphs and larvae. (R. A. C. and R. H.).

Ornithodoros sp. undet.

Host: Yuma bat, *Myotis yumanensis*
Date: September 28 and 30, 1943—3 larvae. (R. A. C.).

Family Ixodidae

Dermacentor occidentalis Marx

Host: Raccoon, *Procyon lotor*
Date: June 8, 1943—1 adult ♀; July 28, 1944—2 nymphs. (R. H.).
Host: Spotted skunk, *Spilogale gracilis*
Date: July 23, 1944—4 larvae, 44 nymphs. (R. H.).
Host: Striped skunk, *Mephitis mephitis*
Date: June 16, 1940—1 nymph. (R. A. C.).
Host: Gray fox, *Urocyon cinereoargenteus*
Date: May 21, 1941—1 adult ♀. (R. A. C.); July 31, 1944—1 larva, 2 nymphs. (R. H.).
Host: California ground squirrel, *Citellus beecheyi*
Date: Taken abundantly from May through August on host as well as from their burrows; nymphs and larvae only. (R. A. C.).
Resting Place: Ground surface or low vegetation.
Date: Adults and nymphs on several occasions from May through August.
Host: Western gray squirrel, *Sciurus griseus*
Date: July 10, 1945—4 nymphs. (R. H.).
Host: California pocket mouse, *Perognathus californicus*
Date: June 20, 1941—4 nymphs; June 27, 1941—15 nymphs. (R. A. C.); July 10, 28, 30; August 22, 1941—a total of 28 nymphs; July 26, 1944—8 nymphs. (R. H.).
Host: Western harvest mouse, *Reithrodontomys megalotis*
Date: July 9, 1943—2 larvae, 1 nymph. (R. H.).
Host: Deer-mouse, *Peromyscus maniculatus*
Date: August 22, 1941—3 nymphs; September 24, 1941—3 nymphs; July —, 1943—55 larvae, 18 nymphs; May 17, 1944—39 larvae; July 18 and 19, 1944—9 larvae, 3 nymphs; September 6, 1944—1 nymph. (R. H.).
Host: Piñon mouse, *Peromyscus truei*
Date: August 21, 1941—1 nymph. Also taken on other occasions. (R. A. C.).

- Host: Desert woodrat, *Neotoma lepida*
 Date: June 10, 1940—2 nymphs; June 12 and 18, 1941—3 nymphs. (R. A. C.); July 6 and 10, 1942—8 nymphs; May 27 and 28, 1943—3 larvae and 4 nymphs. (R. H.). March through August—nymphs.
 Host: Dusky-footed woodrat, *Neotoma fuscipes*
 Date: May, July, August and November—larvae and nymphs. (R. A. C. and R. H.).
 Host: California meadow vole, *Microtus californicus*
 Date: April, July and August—nymphs and larvae. (R. H.).
 Host: Cottontail, *Sylvilagus audubonii*
 Date: June 10, 1944—1 nymph. (R. H.).
 Host: Black-tailed deer, *Odocoileus hemionus*
 Date: September 24, 1942—26 adults; October 6, 1943—1 nymph, 2 ♀♀ and 28 ♂♂; June 2, 1945—7 ♀♀ and 7 ♂♂. (R. H.).
 Host: Horse, *Equus caballus*
 Date: June 9, 1943—11 adults of both sexes. Adults taken again in October and November, 1943. (R. H.).
- Dermacentor albipictus* Packard
 Host: Black-tailed deer, *Odocoileus hemionus*
 Date: September 24, 1942—1 nymph. (R. A. C.); October 6, 1943—23 nymphs and adults. (R. H.).
 Host: Horse, *Equus caballus*
 Date: November 13, 1941—50 nymphs and adults. (R. A. C.); October 1, 1943—1 ♀; October 2, 1943—1 nymph, 4 ♀♀; November 12, 1943—2 ♀♀; November 24, 1943—47 adults, 2 nymphs. (R. H.).
- Ixodes angustus* Neumann
 Host: Piñon mouse, *Peromyscus truei*
 Date: June 19, 1941—1 adult ♀. (R. A. C.).
 Host: Dusky-footed woodrat, *Neotoma fuscipes*
 Date: November 5, 1943—2 adult ♀♀; November 23, 1944—16 nymphs; November 25, 1944—1 adult ♀. (R. H.).
 Host: California meadow vole, *Microtus californicus*
 Date: April 13, 1945—1 adult ♀. (R. H.).
- Ixodes jellisoni* Cooley and Kohls
 Host: California pocket mouse, *Perognathus californicus*
 Date: October through December—adults of both sexes. (R. A. C.).
- Ixodes neotomae* Cooley
 Host: Desert woodrat, *Neotoma lepida*
 Date: October 16, 1940—2 adult ♀♀, 12 nymphs. (R. A. C.).
- Ixodes pacificus* Cooley and Kohls
 Host: Broad-footed mole, *Scapanus latimanus*
 Date: June 21, 1944—2 larvae (R. A. C.).
 Host: Opossum, *Didelphis virginiana*
 Date: June 4, 1941—6 nymphs. (R. A. C.).
 Host: Raccoon, *Procyon lotor*
 Date: June 8, 1943—1 nymph. (R. A. C.).
 Host: California ground squirrel, *Citellus beecheyi*
 Date: March through July—nymphs only. (R. A. C. and R. H.).
 Host: California pocket mouse, *Perognathus californicus*
 Date: June through August—nymphs only. (R. A. C.).
 Host: Deer-mouse, *Peromyscus maniculatus*
 Date: May 1, 1943—1 nymph. (R. H.).
 Host: Western gray squirrel, *Sciurus griseus*
 Date: July 10, 1945, 1 nymph (R. H.).
 Host: Desert woodrat, *Neotoma lepida*
 Date: March 15, 1945—1 larva, 1 adult ♀. (R. A. C.).
 Host: Black-tailed deer, *Odocoileus hemionus*
 Date: December 5, 1943—16 adults of both sexes. (R. H.).
 Host: Horse, *Equus caballus*
 Date: June 9, 1943—1 adult ♀. (R. H.).
 Host: Dog, *Canis familiaris*
 Date: November 18 and 23, 1942—16 adults of both sexes; November 1, 1943—10 adults of both sexes. (R. H.).
 Host: California jay, *Aphelocoma californica*
 Date: June 6, 1943—9 nymphs. (R. A. C.); June 22, 1944—2 nymphs. (R. H.).
 Host: Rufous-crowned sparrow, *Aimophila ruficeps*
 Date: March 31, 1945—3 larvae (R. A. C.).
 Host: Golden-crowned sparrow, *Zonotrichia coronata*
 Date: April 21, 1944—3 larvae; April 21, 1944—2 nymphs. (R. A. C.).
 Host: Whip-tailed lizard, *Cnemidophorus tessellatus*
 Date: June 8, 1941—1 nymph. (R. A. C.).
 Host: Alligator lizard, *Gerrhonotus multi-carinatus*
 Date: May 21, 1941—1 nymph; May 15, 1943—16 larvae, 39 nymphs from one host. (R. A. C.).
 Host: Fence lizard, *Sceloporus occidentalis*
 Date: April 9, 1943—9 larvae, 13 nymphs from one host (R. H.).
- Ixodes rugosus* Bishop
 Host: Spotted skunk, *Spilogale gracilis*
 Date: September 29, 1940—1 adult ♀. (R. A. C.).
 Host: Long-tailed weasel, *Mustela frenata*
 Date: June 9, 1941—25 nymphs. (R. A. C. determination in question.).
- Ixodes sculptus* Neumann
 Host: Spotted skunk, *Spilogale gracilis*
 Date: July 23, 1944—1 adult ♀. (R. H.).
 Host: Gray fox, *Urocyon cinereoargenteus*
 Date: May 25, 1941—1 adult ♀. (R. A. C.).
 Host: California ground squirrel, *Citellus beecheyi*
 Date: Taken in abundance from hosts and burrows. Adults (almost all were ♀♀) in every month except January. Larvae from May through September. Nymphs from March through December. (R. A. C.).
- Ixodes sp.*
 Host: Adorned shrew, *Sorex ornatus*
 Date: November 12, 1941—1 larva. (R. A. C.).
 Host: Trowbridge shrew, *Sorex trowbridgii*
 Date: March 20, 1943—6 larvae. (R. H.). (not *I. soricis*).
 Host: Spotted skunk, *Spilogale gracilis*
 Date: September 30, 1940—4 nymphs. (R. A. C.).
 Host: California pocket mouse, *Perognathus californicus*
 Date: May 12, 1941—3 larvae. (R. A. C.).
 Host: Chaparral mouse, *Peromyscus californicus*
 Date: October 28, 1940—1 larva. (R. A. C.).
 Host: Deer-mouse, *Peromyscus maniculatus* and piñon mouse, *P. truei*
 Date: February through May—larvae and nymphs. (R. A. C. and R. H.).
 Host: Desert woodrat, *Neotoma lepida*
 Date: May 25, 1943 and 1944—larvae; November 25, 1942—1 nymph. (R. H.).
 Host: Dusky-footed woodrat, *Neotoma fuscipes*
 Date: May to November—nymphs. (R. A. C.).
 Host: California meadow vole, *Microtus californicus*
 Date: August 9, 1941—1 nymph. (R. A. C.).
 Host: House mouse, *Mus musculus*
 Date: May 15, 1944—3 larvae. (R. H.).
- Haemaphysalis leporis-palustris* (Packard)
 Host: California ground squirrel, *Citellus beecheyi*

- Date: May 28, 1941—1 ♂ and 1 nymph. (R. H.)
 Host: California jackrabbit, *Lepus californicus*
 Date: June 17, 1944—2 adult ♂ ♂, 23 larvae. (R. H.).
 Host: Cottontail, *Sylvilagus audubonii*
 Date: July 6, 1942—1 adult ♀, 3 adult ♂ ♂, 1 nymph;
 June 10, 1944—23 adult ♀ ♀, 39 adult ♂ ♂, 52 nymphs,
 150 larvae. (R. H.).
 Host: Brush rabbit, *Sylvilagus bachmani*
 Date: May 23, 1941—about 30 adults, 30 nymphs and
 10 larvae. (R. A. C.); May 10, 1943—6 ♀ ♀ and 7
 ♂ ♂. (R. H.).
 Host: California jay, *Aphelocoma californica*.
 Date: June 6 and 9, 1943—13 nymphs, 1 larva; July
 15, 1944—15 larvae. (R. H.).

Family Spinturnicidae

- Spinturnix* sp. undet.
 Host: Yuma bat, *Myotis yumanensis*
 Date: June 16, 1943—several; also found free on the
 roosts at various times. (W. L. J.).

Family Laelaptidae

- Euhaemogamasus liponyssoides* (Ewing)
 Host: Broad-footed mole, *Scapanus latimanus*
 Date: June 21, 1944—3. (D. P. F.).
 Host: California meadow vole, *Microtus californicus*
 Date: March 22, 1945. (D. P. F.).
Euhaemogamasus ambulans (Thorell)
 Host: California meadow vole, *Microtus californicus*
 Date: March 22, 1945. (D. P. F.).
Euhaemogamasus sp.
 Host: California pocket mouse, *Perognathus californi-*
cus
 Date: November 3, 1943—1. (W. L. J.).

Harmalaclaps glasgowi (Ewing)

- Host: California meadow vole, *Microtus californicus*
 Date: From 2 mice March 22, 1945 (D. P. F.).

Laelaps kochi (Koch)

- Host: California meadow vole, *Microtus californicus*
 Date: Nov. 12, 1941—2. (D. P. F.).

Family Trombididae

Trombicula sp.

- Host: California pocket mouse, *Perognathus californi-*
cus
 Date: November 3, 1943—6. (W. L. J.).

Trombicula californica Ewing

- Host: California meadow vole, *Microtus californicus*
 Date: Nov. 12, 1941—1. (J. M. B.).

Family Dermanyssidae

Genus not determined

- Host: Deer-mouse, *Peromyscus maniculatus*
 Date: September 16, 1941—and on several other oc-
 casions. (O. C.).
 Host: California meadow vole, *Microtus californicus*
 Date: September 25, 1941 and on several other occa-
 sions. Also found in mouse nests where they some-
 times numbered in the thousands. (O. C.).

Family Sarcoptidae

Notoedres cati (Hering)

- Host: Bobcat: *Lynx rufus*
 Date: July 27, 1945—50+ (D. P. F.).

Family Macrochelidae

Macrocheles sp. nov.

- Host: California meadow vole, *Microtus californicus*
 Date: March 22, 1945—1. (D. P. F.).

ECOLOGICAL OBSERVATIONS ON THE DISTRIBUTION OF OYSTER LARVAE IN NEW JERSEY ESTUARIES

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INTRODUCTION

According to T. Nelson (1921b and annual reports 1922-1930, and T. Nelson & Perkins 1931) the horizontal distribution of oyster larvae has a direct bearing on the location of natural oyster beds and on the intensity of setting on planted grounds. The distributional pattern of the larvae is ascribed to such factors as (1) the direction and behavior of the prevailing tides, tidal currents and eddies, and the consequent slicks; (2) the position of the beds of spawning oysters with reference to these currents; (3) the direction and force of the prevailing winds, and the relative amounts of turning over of the water; and (4) the vertical distribution of the oyster larvae in the water. With reference to (4) it follows that since the larvae are not distributed uniformly from the surface of the water to the bottom the study of their horizontal distribution is thereby considerably complicated. It is important, then, to know vertical maxima of larval concentrations before definite progress can be made in determining horizontal dispersal. The considerable research which has been performed on the native distribution and behavior of these larvae discloses the need of more detailed observations on their vertical and horizontal movements and the effects of environmental factors on these migrations. Accordingly, the author spent the summers of 1938, 1939, 1940, and part of the summers of 1947 and 1948 in an ecological study of the larvae of the eastern American oyster, *Crassostrea virginica* (Gmelin), emphasizing the vertical migration phase of the problem.

Through the kindness of Prof. T. Nelson, to whom thanks are also due for originally suggesting this problem, the facilities of the New Jersey Oyster Investigation Laboratory were made available. These included a houseboat, the "Cynthia," with marine biological laboratory and living quarters, and a power boat for field work and for towing the house-

boat to the most suitable areas on Barnegat Bay and Great Bay, New Jersey, which were selected for study.

HISTORICAL

The review of the literature relative to this investigation is limited to that of larvae of oviparous oysters. Over the last 4 decades information has been accumulated which suggests that the larvae of *Crassostrea virginica* display certain migratory movements aided by currents and tidal oscillations. J. Nelson (1911) first hypothesized that the larvae of this oyster can control their own distribution by rising and sinking in the tidal streams. Later (1914, 1915, 1916, 1917) he reported additional observations on larval movements in New Jersey estuaries after working out the pelagic stages of the larvae in detail, one of his principal contributions to oyster larvology. And in 1917 he showed in Richmond Bay, Canada, that the larvae do rise during flood tide and sink during the ebb tide, thus migrating away from the ocean.

T. Nelson, also in New Jersey estuaries (1917, 1920, 1921a, 1921b, 1922, 1923, 1924, 1927, 1928, 1930, 1931, 1932), continued the study of oyster larval movements inaugurated by his father. This work was summarized in 1930 (T. Nelson & Perkins): The larvae are herded horizontally into swarms of uneven distribution. These swarms occur in definite lanes up and down stream from spawning oysters and are so distributed by the tidal currents. Where sharp salinity stratification occurs the larvae are to be found in greatest numbers just above the zone of greatest salinity change. When a halocline does not occur the larvae are found vertically in greatest numbers where the current is fastest, behaving as inanimate particles of equivalent density. Applying the results of laboratory studies on larval movements Nelson stated that the larvae, especially

the older stages, drop on, or close to, the bottom during the period of slack water, remain there through the falling salinities of ebb tide and are stimulated to rise by the increasing salinity of early flood tide, thus moving upstream by successive stages.

The Nelsons advanced the following points in support of their theory on the movements of oyster larvae: (1) most larvae were found on the flood tide in estuaries of strong tidal currents and in about equal numbers on the flood and on the ebb tide in those of less currents; (2) the youngest larvae showed no marked differences in vertical distribution, but the older ones tended to stay in the lower strata or on the bottom on the ebb tide, and in the upper strata on the flood tide; (3) in the horizontal plane the earlier larval stages were taken farther downstream and the older stages most abundantly upbay; (4) setting may occur far upstream from spawners, whereas seaward drift of the bay water over a period of 2 weeks would have carried inanimate particles far downstream from the parent beds; (5) since in local estuaries the tide usually runs for a longer time on the ebb than on the flood tide, as a result of stream discharge, there is produced a net drift which tends to carry all freely moving objects oceanwards; the fact that some of the larvae, even though carried seaward on the ebb tide, return to set far upbay would indicate that the larvae are actively swimming for a longer period during flood than during the ebb tide.

Prytherch (1928) and (Galtsoff, Prytherch, & McMillin 1930) in an intensive study found the abundance and distribution of oyster larvae in Milford Harbor, Connecticut, extremely irregular. He concluded that oyster larvae are not passive planktonic forms, that by remaining on the bottom during the greater part of the larval period and by limiting their swimming activities to those phases of the tidal cycle when minimal tidal currents exist, the larvae are able to remain and set in the vicinity of the spawning bed that produced them. Loosanoff & Engle (1940) confirmed Prytherch's earlier findings as to the scarcity of larvae in the Long Island Sound area. Later Loosanoff (1949) reported that in general he found no relation between the stratification of larvae and the stages of the tide and no evidence that larvae in advanced stages of development were more numerous near the bottom. He concluded that in Long Island Sound oyster larvae do not descend to the bottom during periods of rapid tidal flow and are, as a result, widely dispersed by the tidal currents.

Movements and distribution of the larvae of *C. virginica* have been described to a lesser degree by Gates (1910), Stafford (1912), Churchill (1920), and Churchill & Gutsell (1921).

Far fewer observations have been reported on the distribution of the larvae of other oviparous species of oysters. Schaefer (1938) and Elsey (1934; from Baughman 1947) recorded some notes on the distribution of the larvae of *Crassostrea gigas* (Thunberg). Roughley (1933) in his fine paper on *Crassostrea commercialis* (Iredale & Roughley) described the younger larvae of this oyster as moving continuously

from the bottom to the surface, but as they become older generally remain in the lower strata of water.

An analysis of such factors as salinity, current velocity, temperature, light, and pH which may influence the distribution of oyster larvae has been attempted by various investigators in order to determine the fundamental biological conditions which govern larval behavior. T. Nelson & Perkins (1930, 1931, 1932) discovered that oyster larvae are distributed vertically by their own activity in response to salinity changes, to the action of the currents, and to the combination of these 2 factors. Prytherch (1928) in Milford Harbor where tidal currents attain maximum velocities of 46 cm./sec. concluded that oyster larvae settle to the bottom in currents over 15 cm./sec. Contrary to this Loosanoff (1949) noted that in several instances the number of larvae was greatest in currents of maximum velocity. Prytherch's findings are also in striking contrast to those of T. Nelson & Perkins in Barnegat Bay where maximum current velocities are about 25 cm./sec.

As regards the effect of water temperature on the vertical distribution of larvae, J. Nelson (1908, 1916) thought that higher water temperatures cause larvae to rise to the surface and that cold weather drives them down. Perkins (1931) attributed no appreciable influence to temperature in bringing about larval distribution.

J. Nelson (1916), in considering the effect of light on the distribution of larvae, wrote that larvae tend to stay near the bottom at night and to rise when daylight appears. T. Nelson (1926) indicated that eyed larvae are photokinetic, the pallial eyes being of value in causing them to set in shaded areas. Other investigators looking for a phototropic response in the pelagic larvae and finding none have concluded that light is without effect in oyster larvae. Prytherch (1934) stated that he was unable to find evidence which indicates that oyster larvae are sensitive to variations in light intensity or color.

Perkins (1931), attempting to correlate larval distribution and pH, was unable to find any such correlation.

A serious deterrence in much of the research to date on larval distribution has been brought about by the inadequacy, because of lack of equipment and personnel or for other reasons, of consecutive vertical serial sampling throughout the entire cycle of the tide.

GENERAL METHODS

During the course of this work the houseboat laboratory, the "Cynthia," was towed to protected harbors nearest the estuarine areas under investigation. Field observations then were made either from the "Cynthia" or from the motor boat. Such an arrangement has permitted the study of larvae under a wider range of climatic conditions and over a broader geographic range than would have been possible from a single stationary laboratory.

Larval collections were made from the motor boat and with minor modifications were treated as de-

scribed in detail by T. Nelson (1921b). A large brass oscillating clock pump (see photograph, p. 55, T. Nelson 1921b) permanently installed in the motor boat and manipulated manually brought measured quantities of water (usually in 50 liter samples) through a calibrated intake hose from any desired depth down to 5 meters, into a metal drum in the boat. The drum is outfitted with automatic siphons for draining. The water pours into the drum through conically shaped silk bolting cloth nets. A small detachable brass bucket closes the lower tapering end of the net and permits ready removal of the plankton samples to sample bottles. Most of the sampling was performed through 18 XXX silk bolting cloth. Larval samples were preserved in approximately 4% formalin (as recommended by Stafford 1912) and then were ready for identification, counting and measuring. It has been found more recently however that 4% formalin is unnecessarily strong, and that a 1% solution is adequate, disfiguring the specimens less rapidly (Carriker 1950). In the more recent stages of this research the counting of the larvae was greatly facilitated by the use of a multiple laboratory counter. Drawings have been made with the aid of a camera lucida. In the summer of 1947 a new feature was added to the larval sampling gear which made it possible to collect samples off the bottom of the estuary without bringing up sand and mud: a galvanized iron disc approximately 18 inches in diameter with an upturned edge of about one half inch was tied under the small weighted wire cage at the end of the intake hose. Thus when the intake hose with attached sampling disc is lowered to the bottom, and after the sediment raised by the lowering of the gear has been carried off by the tidal current, only those layers of water which are flowing directly over the bottom are taken up, devoid of the sediment which forms such a large portion of estuary bottoms in New Jersey.

With the apparatus described it is possible to sample only one stratum of water at a time. It takes one person from 3 to 4 minutes to take the larval sample, with temperature, salinity and turbidity observations; longer if the current velocity is also observed. Thus in sampling serially a vertical column of water from the surface to the bottom at any given place, the observations given for the bottom strata are as much as a half hour later, depending upon the depth of the water at this point and the frequency of vertical sampling. If the maximum current velocity is appreciable (approximately 23 cm./sec. in the lower Great Bay studies in 1947) considerable water will have passed by the intake hose between the surface and bottom samplings. It is important, then, in the interpretation of these data to keep this method of sampling in mind. The ideal method of sampling would be one in which simultaneous observations for all factors could be made at all strata. It has not been feasible to obtain such equipment, but it is hoped that such observations can be made in the future.

In the determination of salinity, samples of bay

water were brought into the laboratory for titration with standard silver nitrate. American standard sea water prepared by the U. S. Coast Guard and Woods Hole Oceanographic Institution was used as the standard reagent.

In the field, temperatures of the water were taken with a Negretti & Zambra reversing thermometer. In recent summers a Negretti & Zambra continuously recording thermograph has been set up near the laboratory. Also in recent summers a portable automatic tide gage (U. S. Coast and Geodetic model) has been installed for a more close correlation of tides with larval movements. Current velocities of the water were measured in 1947 and 1948 by means of an Eckman water current meter which was standardized by the Bureau of Standards. Limits of visibility in the water were approximated by the use of the Secchi disc and measurement of the volume of wet sediment in given volumes of water was made in some cases. In certain observations the quantity of light reflected by white paper (rectangle 8.5 x 11.0 in.) was determined by the use of a Weston Light Meter which gives readings in candles per square foot. Standard time, recorded in this paper in the Navy system, was checked in recent summers by a portable radio kept aboard the "Cynthia." Depth of water was recorded in the metric system and taken from either the hose, the reversing thermometer chain or the Secchi disc pole, all of which were calibrated. A standard 16-foot shellfisherman's tongs were used in taking samples of the bottom to determine the nature of the bottom and the fixed bottom fauna. More recently a Petersen dredge has been used which serves the same purpose far more effectively. For much of the sampling such observations as the direction (from a standard compass) and velocity (approximate) of the wind and condition of the sky were also recorded. The U. S. Department of Commerce, *Weather Bureau Climatological Data Sheets, New Jersey Section*, have proved useful sources of air temperature and precipitation data.

OBSERVATIONS

NEW JERSEY ESTUARIES

The southern two-thirds of the State is bounded on the east and south by an extensive system of meandering anastomosing brackish waterways which offer the estuarine ecologist a fruitful territory for research, and until recently an area which biologically has been investigated only by the malacologist. These waterways are separated from the Atlantic Ocean by barrier beaches, long low narrow spits of sand, and connect with it by a relatively few deep narrow inlets.

On the landward side a broad marginal strip of salt water marsh, widening to several miles at certain regions, bounds the estuaries. The marshes consist in general of a dominant top cover of salt marsh grass, *Spartina glabra* Muhlenberg; salt meadow grass, *S. patens* (Ait.) Muhlenberg; marsh spike grass, *Distichlis spicata* (L.) Greene; black grass, *Juncus gerardi* Loisel.; and the ribbed mussel, *Modiolus de-*

missus plicatula (Lamarek), over a firm thick mat (many feet thick in some places) of partly decayed grasses, mud, and clay (see also Harshberger 1909, Harshberger & Burns 1919, Martin 1923, Heusser 1949). The grasses and mussels are woven into an unyielding cover which is undermined principally by the tunnelings of the abundant marsh fiddler crabs, *Uca pugnax* (S. I. Smith), swift tidal currents, and wave action. Along the shores of the bays, particularly in the more saline water, the brown alga, *Fucus vesiculosus* Linnaeus, forms a further protective mat against the forces of erosion. It is this wearing away of the shoreline and soft bottom material together with the accumulation of the fecal pellets of molluscs and other invertebrates which supplies the detritus so bothersome during rough weather in the study of plankton samples. The salt marsh snails, *Melampus lineatus* (Say) are abundant in the grasses near the high water mark.

An abundant and probably a very important supply of microscopic food flourishes on the surface of the fertile marsh mud, protected from erosion by the stand of grasses, yet receiving ample sunlight. The marshes, though well covered by the high spring tides, are well drained by an elaborate system of mosquito ditches which facilitate good circulation of bay water over them. This in turn promotes more rapid transport of the microscopic food which is picked up off the mud during high water and passes out with the ebb tide to the plankton feeders in the estuaries (Martin 1923).

Numerous creeks and rivers drain the flat eastern hinterland of the area, bearing in the effluent leachings which play a part in the fertilization of the tidal basins and the marshes. Just how significant in fertilization these substances are, and in turn the extent to which the microscopic food supply from the marshes influences the productivity of the estuaries yet remains to be investigated. T. Nelson (1940-41) in preliminary studies in this direction finds that streams in southern New Jersey are high in organic or bog iron and experiments in his laboratory confirm earlier work on the stimulating effect of such stream water upon diatom growth.

There are some indications that the cedar water which these streams carry during periods of heavy rainfall may be harmful to some members of the estuarine community. This phase of estuarine ecology merits further investigation. According to Stone (1911) the white cedar, *Chamaecyparis thyoides* (Linnaeus), next to the pitch pine, is the most characteristic tree of southern New Jersey, following the courses of all the streams and spreading out in many places to form immense cedar swamps. During excessively rainy periods the water from these swamps, which is colored a characteristic dark coffee color, pours down the streams into the estuaries, imparting this color to the surface waters of entire bays at a time.

The bottoms of the estuaries themselves are composed of a mixture of fine black silt and sand which may range from a preponderance of thick silt de-

posits on bottoms of relatively little water current to firm fine clear sand in channels of greater water movement. Over the years the shells of *Ostrea* and of *Venus* and of other Mollusca in lesser numbers have accumulated on many of these bottoms where stones and other hard objects are entirely lacking. The eel grass *Zostera marina* Linnaeus, once reported to have flourished in these bays (Stone 1911), practically disappeared in 1931, but now is reappearing in small quantities in some of the estuaries such as upper Barnegat Bay.

The dominant bivalves on these bottoms are *C. virginica* (Gmelin) and *Venus mercenaria* Linnaeus. *Mya arenaria* Linnaeus, *Gemma gemma* (Totten), *Mytilus edulis* Linnaeus (near the inlets), *Solen viridis* Say, *Siliqua costata* (Say), *Ensis directus* (Conrad), *Tellina tenera* Say, *Spisula solidissima* (Dillwyn), *Barnea truncata* (Say) occur in less numbers; occasionally *Petricola pholadiformis* Lamarek, *Collocardia morrhuana* (Linsley), *Arca campechiensis pexata* Say, and *Anomia simplex* d'Orbigny are collected. The dominant gastropods are *Urosalpinx cinerea* (Say), *Nassa obsoleta* (Say), *Polinices duplicata* (Say). *Busycon canaliculatum* (Linnaeus), *B. caricum* (Gmelin), *Eupleura caudata* (Say), *Polinices heros* (Say), and *Crepidula fornicata* (Linnaeus) are less numerous. These lists include only commoner forms; there is urgent need for detailed ecological surveys of these waters with detailed listings of the fauna and flora. In this connection the reports of Wood & Wood (1927) and Richards (1938) are useful.

Other conspicuous invertebrate members of these bottom estuarine communities are the numerous and predacious *Callinectes sapidus* Rathbun, the common *Palaemonetes vulgaris* (Say) so abundant along the shorelines, the mud-tube dwelling *Ampelisca* sp. whose small flattened mud tunnels may appear in such numbers on the surface of the bottom mud as to resemble black grass, *Limulus polyphemus* Linnaeus, *Cliona celata* Grant, and *Microciona prolifera* (Verrill).

In the warmer months of the year bivalve larvae constitute a major portion of the plankton of these bays. Soon after periods of pelecypod spawning, the larvae may appear by the thousands per hundred liters of water, quite eclipsing the algal, protozoan, annelid, gastropod and crustacean plankters which form the dominant part of this rich pelagic association. However, one of the serious obstacles facing the bivalve larvologist is the dearth in the literature of keys for the proper identification of the larvae. In Europe the fine beginning which Jørgensen (Thorson 1946) has made on a study of the older stages of the larvae of Danish marine bivalves, and the contributions which Lebour (1938, and other years) has made on the bivalve larvae of English waters, are of considerable help. In America we have principally the very useful paper of Stafford (1912) which describes and illustrates several of the commoner bivalve larvae, Wells' (1927) photomicrographs of the various stages of the same larvae, and

more recently the valuable contribution of Sullivan (1948) which describes and illustrates the bivalve larvae of Malpeque Bay, Canada.

In New Jersey we are certain of the identification of the larval stages of *Crassostrea virginica*, *Venus mercenaria*, *Mytilus edulis*, *Modiolus demissus*, *Mya arenaria*, *Teredo navalis* Linnaeus, *Anomia simplex* and *Gemma gemma*. Nevertheless there are present in the water at one time or another during the summer months all of the stages of other bivalve larvae whose identification is questionable or has not been possible, and some of whose stages are very similar to those of larvae already identified.

In the winter months in New Jersey the larvae of *Mytilus edulis*, as also reported for Danish waters by Jørgensen, Thorson (1946), are present in the bays in considerable numbers. Other species are also encountered though in negligible numbers. In this connection the paper by Engle and Loosanoff (1944) on the setting of *Mytilus* larvae in Milford reports the maximum intensity of setting as occurring on June 29-July 6. No mention is made of the seasonal distribution of the *Mytilus* larvae, though from earlier histological examination of the gonads of mussels it is pointed out that mussels in Milford begin spawning when the temperature approaches 60° F.

The unidentified bivalve larvae in our waters probably belong to such pelecypods as *Arca*, *Pecten*, *Modiolus*, *Cardium*, *Dosinia*, *Petricola*, *Tellina*, *Macoma*, *Donax*, *Tagelus*, *Solen*, *Ensis*, *Siliqua*, *Barnea*, *Zirfaea*, *Bankia*, *Spisula*, and others, which are known to occur in the estuaries or along the inshore areas of the Atlantic Ocean.

It can be seen, therefore, that there is a fundamental need for further work on the artificial fertilization and culture of bivalve larvae as a means toward the proper identification and description of pelecypod larvae, such research being basic to any future morphological, physiological or ecological study of these prodissoconchs.

IDENTIFICATION OF OYSTER LARVAE

Among the numerous papers on *C. virginica*, the following include descriptions and/or illustrations of oyster larvae: Brooks (1880), Jackson (1888), Stafford (1905, 1909, 1912, 1913), J. Nelson (1909, 1910), Churchill (1920), T. Nelson (1921b, 1923), Wells (1927), Prytherch (1934), Medcof (1939), and Sullivan (1948). The illustrations are given in the form of photomicrographs, pencil or pen-and-ink drawings, and the majority of them are of the older stages of the larvae. J. Nelson (1909), the first to publish photomicrographs of oyster larvae, T. Nelson (1921b), Wells (1927) and Sullivan (1948) in photomicrographic form illustrate the various stages of the larvae, yet much of diagnostic detail is lost in such reproduction. Stafford (1912) has drawn the various stages and included some internal structure; however, internal structure is not always readily apparent in fresh samples or in formalized larvae. Thus pen-and-ink drawings of the principal stages of the larvae which stress the diagnostic external contours of the valves might be used to supplement

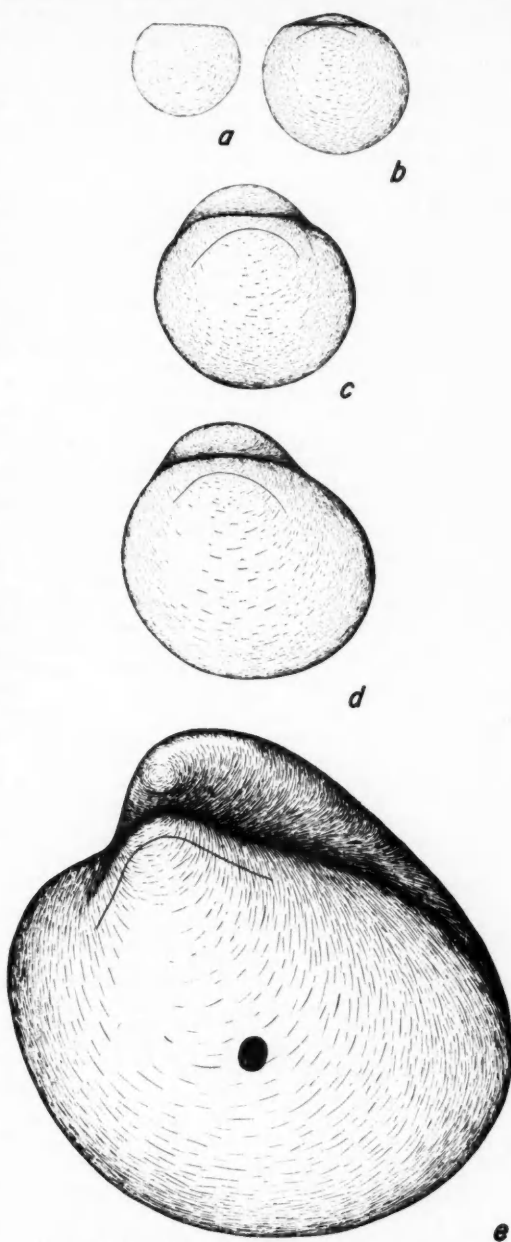


FIG. 1. Pen-and-ink drawings of various stages of the larvae of *C. virginica*, stressing the diagnostic external contours of the valves. The lengths, in micra, of the larvae are as follows: a, 62; b, 82; c, 111; d, 140; e, 284. All drawings 270X.

photomicrographs in larval identification. Such an attempt has been made in Figures 1 a-e, which were drawn from freshly preserved larvae under the camera lucida. The veligers were collected in the summer of 1948 in Little Egg Harbor.

In New Jersey waters the length of oyster larvae varies from approximately 60 μ in the earliest stage at which the valves completely clothe the veliger to approximately 300 μ at the time of setting, as also reported by T. Nelson (1921b). The largest larva obtained during my own studies was 306 μ long and was collected in Great Bay. T. Nelson (1923, p. 329) gives a curve illustrating the rate of growth of oyster larvae in Barnegat Bay in June, in which the oldest larvae measured 248 μ in length. Prytherch (1934) records an average dimension for fully grown larvae in Milford Harbor, Connecticut, of 330 x 220 μ . In Canadian waters Stafford records the maximum size of larvae at 358 x 365 μ (in 1905) and later (1912) 369 x 384 μ ; J. Nelson (1917), at 320 to 400; and Medeof (1939) at 365. The variation in these dimensions suggests a possible study of the distribution of the maximum size range of oyster larvae along the Atlantic seaboard from the Gulf of Mexico to Canada; if as T. Nelson (1921b) suggests, the larger maximum size of the Canadian larvae is due to lower water temperatures, then one would expect to find relatively smaller larvae in Delaware Bay, N. J., and still smaller larvae in the Gulf of Mexico.

In Table 1 are given the range of measurements of oyster larvae through the larval cycle, taken from several swarms in Little Egg Harbor during August and September, 1948. Length, height, and length of hinge line (if measurable), in this order, are recorded. Some variation can be seen from the table in the length-height ratio, and it may be noted that the first appearance of the "eyed" condition in relation to size is also rather variable.

TABLE 1. Range of measurements (length, height, hinge line if measurable) in μ of the various stages of oyster larvae taken at random in Little Egg Harbor, N. J.

<i>Straight Hinge</i>	<i>Early Umbo</i>	<i>Late Umbo</i>	<i>Mature</i>	<i>Eyed</i>
62 x 55 x 40	82 x 77	153 x 157	220 x 220	262 x 262
62 x 52 x 40	88 x 88	153 x 163	224 x 224	260 x 266
62 x 52 x 38	91 x 94	175 x 175	252 x 252	266 x 270
67 x 59 x 40	95 x 91	185 x 200	252 x 266	273 x 266
75 x 69 x 44	99 x 105	196 x 203	262 x 266	270 x 252
77 x 77	117 x 124	217 x 234	270 x 266	280 x 273
	124 x 126			284 x 273
	127 x 127			
	132 x 135			
	134 x 138			
	140 x 145			
	144 x 144			

LARVAL CYCLE OF *C. VIRGINICA*

A brief review of the prodissoconch period (taken principally from W. K. Brooks, Jackson, J. Nelson and T. Nelson) may make clearer the evidence for the native movements of the larvae. It is thought that sexually mature oysters spawn on the late flood tide (T. Nelson, 1921, 1922, 1927; Prytherch, 1928), the total annual production by one female being estimated at 50-60 million eggs (see discussion by Burkenroad 1947). Sperm and ova are thrown into the

bottom strata of the water where fertilization occurs. Ova sink at least an inch in 7 minutes after oviposition, and the early embryos develop cilia in 4 or 5 hours. In currents of 13 cm./sec. or more, they may be carried some distance. After the cilia form, most of the embryos crowd to the surface of the water, in part pursuing an active spiral progression. About a day after fertilization the embryos, now larvae with complete purse-shaped valves, are recognizable as straight hinge larvae; in New Jersey waters they measure approximately 60 μ in length and swimming actively soon become distributed vertically. In about 2 weeks from the time of fertilization and at a water temperature of approximately 27° C. these veligers pass through the stages arbitrarily designated as early umbo, late umbo, mature, and eyed larvae. Mature and eyed larvae are relatively more powerful swimmers than the younger larvae, and although they are unable to make much headway against a current, may rise in less than an hour from the bottom to the surface of shallow bays in response to such environmental factors as steep salinity gradients and fast currents. After careful selection of the proper attachment site, in or during relatively still water, the eyed larvae cement themselves to firm clean surfaces. They are then known as spat.

LANOKA LAGOON, BARNEGAT BAY

The study of the movements of oyster larvae was first undertaken in this small shallow arm of Barnegat Bay in the summer of 1938. The Lagoon is approximately 0.2 mile wide and 1.7 miles in length, running in an east-west direction, and empties to the east into Barnegat Bay. It has an average depth at mean low water of 2 to 3 feet, the mean range of the tide is 0.6 foot and the spring range, 0.7 foot. The rather level bottom consists of a thick deposit of black silt. A narrow zone of salt marsh rims the southern shore. There was no pollution at the time of the observations. A small stream, Cedar Creek, empties into the west end of the Lagoon, and is well named since in times of heavy rains large quantities of cedar water are brought down by it. The laboratory was moored in a small cove in the middle of the southern shore of the Lagoon, and most of the observations of the summer were made off West Point, just outside the cove.

Water currents are relatively slow in the Lagoon and in Barnegat Bay. No current velocities were determined, but Perkins (1931) obtained maximum current velocities of the water in Barnegat Bay of approximately 25 cm./sec., though most of his figures were considerably lower than this. Thermal and saline stratification in the Lagoon are pronounced in calm weather. During flood tides the saltiest water creeps in nearest the floor of the estuary, and the fresh water from Cedar Creek pours seaward over the surface during both the flood and the ebb. The flow of water over the bottom is retarded by friction from the bottom.

Rainfall in June and July of this summer was the heaviest in the State since the beginning of the rec-

ord, while August was relatively dry: there was continuous stormy weather from July 11 to August 8. The unusual volume of fresh water from rain caused surface salinities to remain extremely low (between 0.5 and 6.0 ‰ at West Point from July 18 to August 12) and brought quantities of cedar water into the Lagoon. Bottom salinities ranged from 12 to 22 ‰ through the summer. Air temperatures for June were slightly below normal, for July slightly above normal, and for August very much above normal; water temperatures tended to reflect the air temperatures, a conspicuous trend in these shallow bays.

Very few oysters were found in the Lagoon itself: thus most of the oyster larvae observed in these studies were those carried in by the tidal currents from the oyster beds in Barnegat Bay. The heaviest spawning of the season occurred on July 27, preceded by stormy weather and slightly rising water temperatures, and followed by 12 days of practically uninterrupted storms. Minor spawnings occurred on August 1-3 and 7. The second largest spawning of the season took place on August 14, preceded by clear and warm weather.

Thus when the first study was made of the movements of the larvae through the cycle of the tide on August 16, the most abundant stages present were the early umbos. This day was selected as it coincided with the ebb slack in the early morning, was calm and clear, and there were numerous larvae in the Bay. The powered collecting boat was anchored securely off West Point and 71 plankton samples representing 100 liters of bay water each were pumped hourly through the 12 hours of the flooding and ebbing tide at vertical distances of 0.2 meter from the surface of the water. As nearly simultaneously as possible, observations were made on meteorological conditions, tide level, salinity, temperature, and turbidity of the water.

The data taken in the observations are plotted in Figure 2. Each vertical hourly (slanting) column, bordered by faint dotted lines, represents the results of observations made on each column of bay water. It includes the logarithms of the numbers of the various stages of oyster larvae per 100 liters of bay water and the salinity and temperature curves. Meteorological observations are indicated across the top of the columns. An attempt has also been made to connect by incomplete curves the maximum concentrations of the earlier more numerous larvae in each column.

These data indicate that all stages of the larvae did not flow past a given point uniformly distributed, but were unequally spaced both horizontally and vertically. In addition the separate larval stages tended to follow an independent distribution pattern as they matured. Larval concentrations did not taper linearly from maximum concentrations toward surface or bottom, but unexpected pockets as well as gradual diminution of larval numbers occurred in all planes.

The maximum number of all stages of oyster larvae counted in any one sample was 762. The straight

hinge and early umbo larvae occurred fairly evenly distributed from surface to bottom at 0830 with slight concentration at 0.6 meter. Through the early flood they were found near the surface and near the bottom, concentrating most heavily toward bottom on the late flood and flood slack. On the early ebb they spread surfaceward and on the mid ebb appeared abruptly in marked concentrations at 0.4 meter. The late umbos in most instances remained in the deeper half of the vertical columns. Mature larvae were found broadly distributed but distribution was very spotty. Eyed larvae (very few in number) were present only on the flood (at 0830, 0930 and 2030 samplings) and principally in the surface strata.

Well formed haliclines occurred during the first 6 hours, diminishing somewhat on the ebb. At 0830 and 0930 the greatest concentration of straight hinge and early umbo larvae occurred just above the halicline; in much of the remainder of the flood and first half of the ebb the salinities above the halicline were very low (lowest at 1330, 4.34 ‰) possibly tending to repel the larvae from this stratum. Along the bottom, salinities never dropped below 15 ‰. Although nothing is known of the effect of cedar water on estuarine life, the presence of a high concentration of cedar water in the surface stratum of the Lagoon at this time must not be lost sight of as one of the possible factors in explaining the distribution of the larvae. At 1630 and 1730 the larvae were again noticeably aggregated in the zone of the greatest salinity change. Attention is directed to the fact that during the early flood the halicline was elevated by the incoming flood of saltier water beneath, and that even before the termination of the seaward flow of the bulk of the water toward the end of the day, the water along the bottom was already becoming saltier at 1930, indicating a change from the ebb to the flood current there even as the surface water was ebbing.

On this day the more saline water coming into Lagoon Lagoon was somewhat cooler than the surface water pushing bayward from Cedar Creek, and correspondingly the halicline and thermocline coincided throughout the hourly collections.

The wind was negligible throughout the day, minimizing the mixing of the water and permitting the formation of distinct haliclines. The sky was overcast with the exception of a short period at 1530 and 1630. It may be worth pointing out that pockets of larvae appeared high in the vertical column at 1630 and 1730; insufficient information is available as yet to permit the suggestion that light may have been partly influential in bringing about this distribution.

Although the study made on August 16 was the only one in the summer of 1938 in which consecutive vertical serial samplings were made throughout the cycle of the tide, some 25 single vertical serial samplings were made off and on throughout the summer. In these when sharp haliclines occurred, the greatest larval concentrations (primarily early stages) did not always show a constant distribution with respect to the halicline, being found with some frequency be-

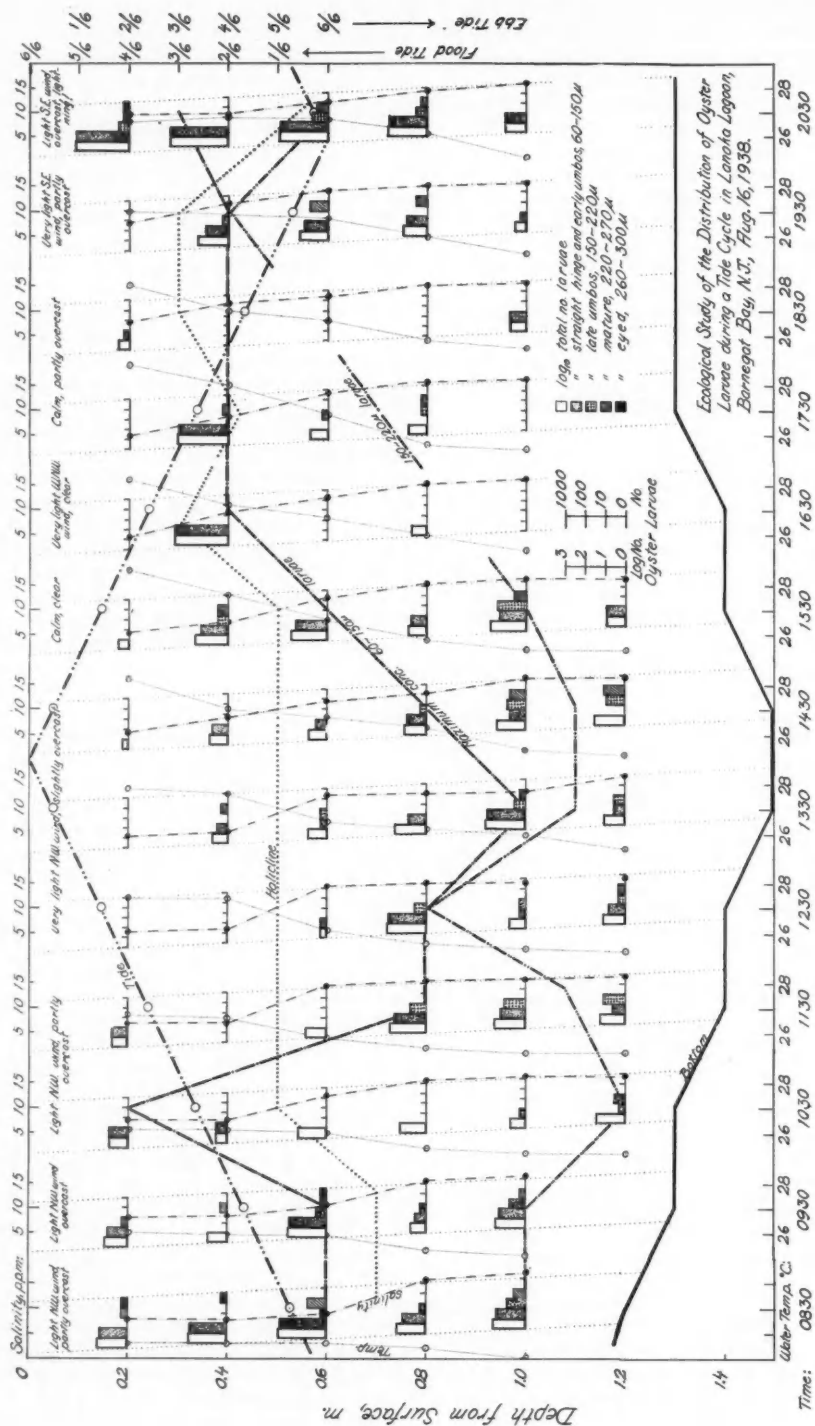


FIG. 2. The Lanoka Lagoon tidal study.

low, in or above it, and often diminishing in numbers upward or downward far from the halicline into salinities on the bottom as high as 22.0 ‰ and in the surface as low as 3.10 ‰. Finding the larvae in such low salinities is a measure of how far upbay they may move in their migrations into the headwaters of the estuaries. Below are given the actual salinities and the number of straight hinge, early and late umbo larvae found at various times in some of these salinities per 100 liters of water. Also, roughly indicated are the quantities of cedar water present (xxx, excessive; xx, moderate; x, slight amounts as indicated by the color of the water sample) in each larval sample during periods of excessive rainfall.

Salinity ‰	No. Larvae	Cedar Water
3.1	5	xxx
3.6	18	xx
3.7	2	xxx
4.3	10	
5.5	120	
5.0	6	x
5.2	6	xx
6.9	408	xxx
7.1	180	xx
7.5	644	xx
8.3	64	xxx
8.5	282	x
9.5	762	
9.5	1390	x
10.0	1014	x
10.8	1668	
13.3	416	x

One or 2 larvae were found occasionally in salinities as low as 0.85 ‰, but these may have been contaminants from previous samplings. The maximum concentrations of larvae taken throughout the summer in vertical samplings occurred in a salinity range of 7.5 to 20.0 ‰. The figures in the preceding table demonstrate to what extent the larvae may penetrate the cedar water, but it is difficult to separate the effects of salinity and cedar water on larval movements in this case where the fresh water is the solvent for substances from the cedar swamps. The maximum concentrations of larvae taken throughout the summer were pumped from a depth range in meters of 0.2/1.0 to 1.2/0.3 (where the numerator expresses the depth at which the sample is pumped, and the denominator the remaining distance to the bottom), and the majority of these concentrations were found in the middle strata of the water. No samples were pumped off the bottom. The temperature of the water from which larvae were pumped during the summer ranged from 20 to 32° C.; the limits of visibility as measured with the Secchi disc, ranged from 0.4 to 0.8 meter.

GREAT BAY

This estuary was chosen as the next site for a continuation of the study of the movements of oyster larvae principally because of the contrasting ecological conditions present there as compared to those found in Barnegat Bay.

Great Bay is one of the largest open estuaries on the eastern coast of the State, measuring approxi-

mately 7.5 statute miles in length from the mouth of the Mullica River at Deep Point on the northwest to Little Egg Harbor Inlet on the southeast, and is 4.3 miles across at its widest portion. It has an average depth at mean low water of about 4 to 7 feet, which deepens to 35 feet at Deep Point and to 40 feet at Little Egg Inlet. The Bay is also connected with estuaries to the north (Little Egg Harbor) and to the south (Little Bay) by a complicated maze of channels and waterways. The mean range of the tide recorded for the upper end of the Bay is 3.4 feet, and the spring range, 4.1 feet. Current velocities as high as 52 cm./sec. have been recorded in some of the tidal creeks leading into Great Bay; out in the broadest portion of the Bay the maximum velocities approximated 25 cm./sec. Because of the configuration of the bottom and of the channels leading into the Bay, and because of swift tidal currents, considerable mixing of the water occurs. Consequently halicline formation is negligible and waters are highly turbid especially in the tidal creeks leading into Great Bay. By the time the water reaches the broader shoaler portions of the Bay it has lost much of its sediment and Secchi disc readings of 1.8 meters have been obtained. The bottom of the Bay is composed of a variety of sediments ranging from black silt to firm sand and gravel mixed with various amounts of silt. These firmer bottoms make excellent oyster grounds and contribute materially in the production of significant yields of oysters in this area. The Mullica River, some 0.3 mile wide and 30 feet deep in its lower reaches, and its tributaries pour the effluent drained from a broad area of flat land northwestward about 30 miles into the Bay. The quantities of cedar water received by Great Bay during rainy periods are as concentrated as those observed in Lanoka Lagoon, though more conspicuous because of the greater volumes of water involved. A broad marginal strip of salt marshland some 1 to 2 miles in width bounds the Bay on all sides. The Bay is unpolluted; only a few small villages hug the shores of the Mullica, its tributaries, and some of the tidal creeks from the Bay. Considerable small boat traffic occurs during the summer, but did not interfere with plankton studies.

Summer of 1939

Larval studies were conducted in the vicinity of Turtle Island where mature oysters were abundant on firm bottom. The summer proved a poor year for oyster larvae. Low temperatures in July, storms, strong winds, severe and sudden temperature changes, and an abundance of *Nemopsis bachei* Agassiz explain in part the relatively small number of larvae encountered. Through the summer the salinities in the Turtle Island area averaged between 19 and 27 ‰; yet an extreme northeast storm in August so reduced salinities in this region as to make surface water drinkable.

Out of the observations of the summer on the larvae two series of samplings are worth recording. On July 5 plankton samples were taken vertically at 0.2

meter intervals in water 1.4 meters deep just off the northwest end of Turtle Island, where the current is somewhat reduced on the flood in passing between the island and the mainland. It was 0830, half flood tide, a clear day, and the wind was blowing briskly from the south; however, Turtle Island protected the sampling site from wave action. Temperature and salinity were practically constant between surface and bottom. Numerous straight hinge and a few early umbo oyster larvae were present, concentrated in the deeper half of the water. The total larval counts per 100 liters of water starting with the surface sample were: 3730, 2640, 2500, 8500, 8700, 7250. No explanation is offered for this distribution since there was no apparent correlation with the ecological factors observed.

On July 10 a series of vertical samples was taken in 1.4 meters of water on the south side of Turtle Island in the full sweep of the early flood tide passing into the Mullica River. The darker, fresher river water (16.7‰; 25.7° C.) was still flowing seaward on the surface while the lower more saline water (25.0‰; 23.0° C.) was already flooding. It was 0945, a clear day and a very light wind was blowing from the west. A tide rip was seen to pass under the boat upstream as samples were being pumped from the 0.8 meter stratum. As soon as the vertical series of samplings was completed a second vertical series was taken at 0.2 meter (21.5‰; 24.6° C.) and at 0.6 meter (24.7‰; 23.5° C.). In the first vertical series the counts of straight hinge, early and late umbo oyster larvae per stratum starting with the surface were: 46, 264, 110, 112, 34, 48, and 104. The greatest concentration of larvae was found just above the halicline where the salinity difference between the two strata was 6.2‰. In the second vertical samplings the larvae were predominantly in the surface stratum, again above a halicline, the counts at 0.2 meter being 1336 and at 0.6 meter 300 larvae! A suggested explanation for this abundance of larvae in the surface water behind the tide rip is that the larvae were stimulated to rise not only by the flooding water as they generally do, but also by the increasing salinities and by the turbulence of the water in the tide rip. It is impossible to say whether the slight thermoclines present did not also play a part in distribution, since no results on the effect of temperature gradients on larval movements are available.

Summer of 1940

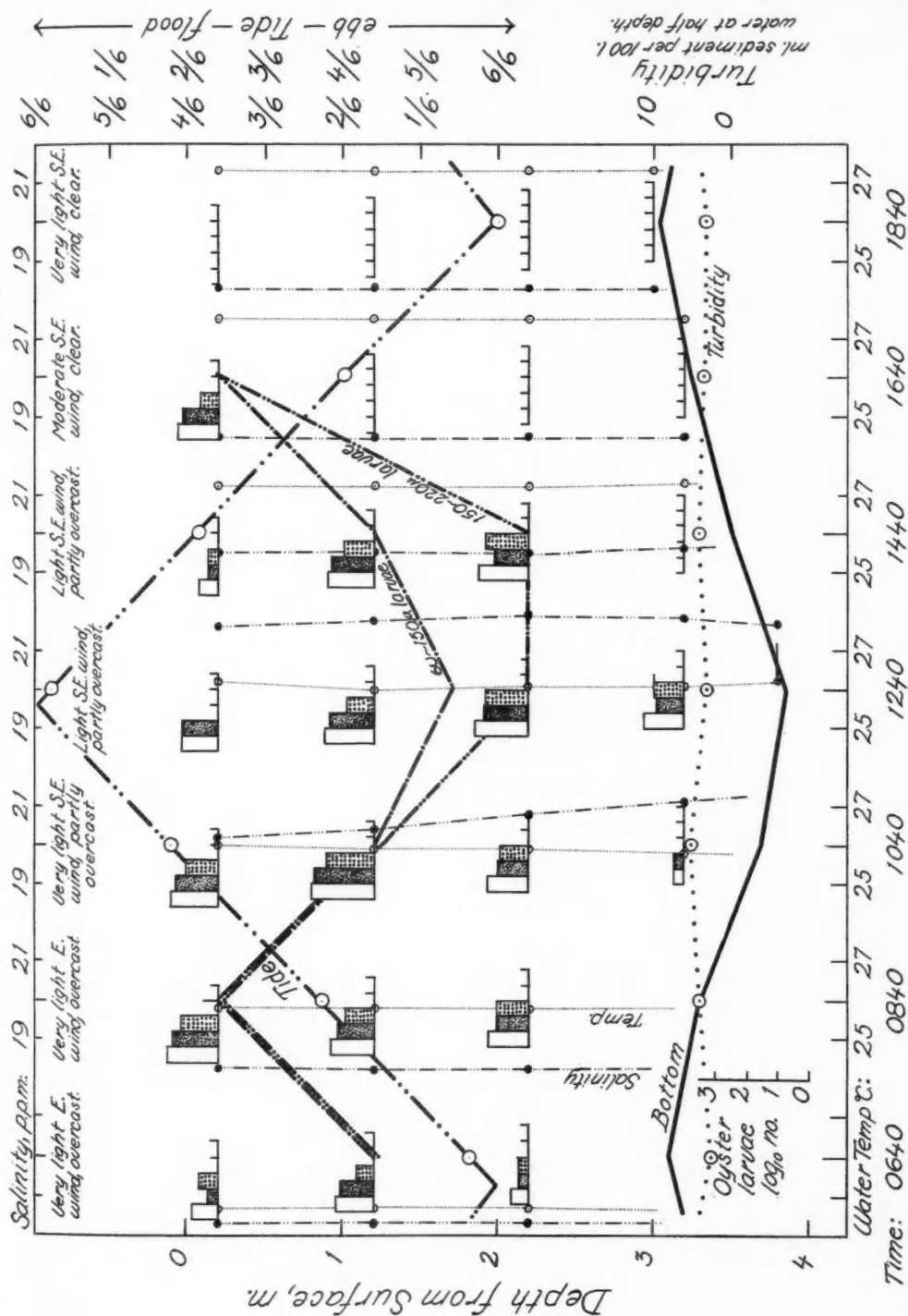
This summer produced more oyster larvae than the previous one, making possible the study of larval distribution through the cycles of two separate tides.

June and the early part of July were cool, but air temperatures showed a decided climb during the latter part of July, only to drop again in August. Water temperatures in the Turtle Island area rose from an approximate low of 19° C. in the early part of July to occasional peaks of 30° C. in the end of July and the first part of August, and then dropped gradually to a low of 20° C. toward the end of Au-

gust. Precipitation was decidedly deficient in July; by contrast August was a wet month. Correspondingly, average salinities in the first week of July ranging from 10-19‰ gradually rose to 20-25‰ in the second week in August and then dropped to 16-21‰ during the last few days of August. Spawnings followed by conspicuous numbers of larvae occurred on July 8, 18, 20, 26 and 30 and August 5, 6, 11, 12 and 21. The largest counts of straight hinge larvae were found after the spawnings of July 18, 20 and 30, with counts as high as 11,500 larvae per 100 liters of water!

Winter Creek. On July 24 with early and late umbo larvae in the water, fair weather and ebb slack coming in the early morning, the opportunity was presented for the first study in this area of the larvae through the cycle of the tide. Sampling was done from the motor boat which was tied to the "Cynthia" in Winter Creek, at a bend in the stream where the tide has gouged out a relatively deep pocket. A shoal mud bar partly blocks the entrance to Winter Creek at low water. Thus through a combination of a shallow entrance, the winding creek and the deep pocket at which sampling was performed, the water in the creek is thoroughly mixed. Further, since the creek drains only salt marsh, normal salinity ranges remain unaltered except during periods of rainfall. Pumping was started at 0640 and 27 plankton samples were collected every 2 hours through the flood and ebb of the tide at vertical intervals of 1.0 meter from the surface. At the same time observations were made on meteorological conditions, tide level, salinity, temperature and turbidity. Samplings at each stratum consumed about 4 minutes. The data are plotted in Figure 3 where this time no attempt is made to show the slanting nature of the vertical columns. The maximum number of larvae counted in any one sample was 96, a number which compared to the 11,500 larvae counted in a sample at the head of Great Bay only 2 days before is small. This trend, the presence of fewer larvae in the creeks, has been observed throughout my larval studies in New Jersey estuaries.

Examination of Figure 3 shows an uneven distribution of the larvae both vertically and horizontally, this despite the considerable mixing of the water that takes place in Winter Creek. The greatest concentration of early umbos rose from an intermediate stratum at low water to the surface layers during full flood, dropped somewhat during flood slack and early ebb, and rose again to an exclusive surface position in mid ebb. The blank column at 1840 illustrates the total absence of larvae beyond the boundaries of the particular larval swarm present in these waters at that time. This swarm apparently was widely distributed in the horizontal tidal stream, coming past the boat in small numbers at 0640, this number increasing up to flood slack, then decreasing to zero at 1840. Less larvae have generally been found on the ebb tide than on the flood in these New Jersey studies. This may be accounted for in part by the inroads of gill-feeding animals.



Ecological Study of the Distribution of Oyster Larvae during a Tide Cycle in Winter Creek, upper Great Bay, N.J., July 24, 1940.

FIG. 3. The Winter Creek tidal study.

The later umbo larvae appeared to follow the same distribution as the early stages except that during flood slack and early ebb their zone of greatest concentration occurred in a deeper stratum of water.

In an attempted explanation of these vertical larval movements, temperature (range during the day: 24.7-27.5° C.) and salinity (range from low to high water: 18.2-21.9 ‰), because of their constancy from surface to bottom, can be ruled out as possible factors; light should not be entirely excluded as by 1640, when the larvae swarmed at the surface, the sky which had hitherto been overcast, became clear. Also shortly before 1640 a brisk wind sprang up increasing wave action and agitation of the surface water. Perkins demonstrated (T. Nelson and Perkins 1931) that increase of larvae near the surface may be caused by wind currents there. Turbidity again is an unknown factor, yet indicates those phases of the tide when currents were swiftest, faster currents raising greater quantities of inert material. There is some indication that the majority of the larvae in these observations (mostly early stages) were stimulated to remain in the higher levels of the water at the time of the swiftest currents which occurred at approximately mid flood and mid ebb. As noted also in the Lanoka studies, a differential behavior was displayed by the older larvae, which lagged in the deeper water at 1240 and 1440.

On July 22 at 1100 a single vertical series of samples was pumped in Winter Creek beside the "Cynthia" at intervals of 1 meter and in the very late flood. These produced what was for Winter Creek a relatively large number of larvae. A light northwest wind was blowing and the day was clear and hot. Temperature (26.6-26.5° C.) and salinity (20.4-20.5 ‰) were practically constant between surface and bottom. The following early umbo larvae, starting with the surface sample, were obtained: 600, 900, 300 and 100; late umbo larvae; 120, 200, 100, 25. According to the phase of the tide this vertical column if placed with the data in Figure 3, would fall in the 1240 column, and the stratum of greatest larval concentration in the July 22 column coincides rather well with the larval curve indicated in Figure 3, falling only slightly above the larval curve.

Turtle Island Bed. A second study was carried out on August 7, similar to the one executed in Winter Creek, over the Turtle Island oyster beds, a few hundred yards out in deep water and directly below the mouth of the Mullica River where the water from the Bay is bottle-necked into a deep narrow stream. The bottom deepens gradually at this point from Great Bay into the Mullica River, and considerable mixing of the water occurs particularly on the ebb as the water pours out of the Mullica River. The motor boat was anchored securely and maintained in the same position all day. Variable weather conditions were encountered: hard rain, thunder showers, clear. Observations were made on meteorological conditions, tide level, salinity, temperature, turbidity

and plankton. Samples were pumped hourly and at 0.5 meter intervals from the surface. Samplings at each stratum consumed about 4 minutes. Seventy-five consecutive plankton observations were made starting with low water at 0620 and continuing through flood slack to low water again at 1820. The maximum number of larvae encountered in any one sample per 100 liters of water in the course of the tidal study was 2,144. By far the majority of the larvae were straight hinged coming from the August 5 and 6 spawnings. In addition as many as 24 eyed larvae per 100 liters of water were found in the 0820 samples. The data are presented in Figure 4.

Inspection of Figure 4 again discloses a marked uneven vertical and horizontal distribution of the larvae in spite of excessive mixing of the water. A fairly pronounced rising of the densest aggregation of the straight hinge larvae toward the surface occurred during flood tide; a fairly even vertical distribution was evident during late flood (1120) with greatest concentration at 1.5 meters; a notable single concentration appeared at flood slack at 1.5 and 2.0 meters; on the ebb the larvae rose precipitously into the surface layers, and dropped slightly at ebb slack. A singular instance of a large concentration of straight hinge larvae was met at the surface at 1820, somewhat similar to that found in the Lanoka Lagoon study.

The mature and eyed larvae appeared in the surface layers of the water at mid flood, a few were found again during late flood in the deeper water; and none were encountered during ebb. The larvae on this day were distributed horizontally in two separate larger swarms as suggested by the absence of larvae at 1020 and 1620.

As in the Winter Creek study, temperature (range during the day: 25.2-25.6° C.) and salinity (range from low to high water: 20.3-27.2 ‰) were relatively constant between surface and bottom in any one vertical column. When the larvae concentrated in the surface stratum during the ebb at 1420 and 1820, the sky, which during most of the day was overcast, became clear; the correlation (or coincidence?) is particularly noticeable at 1820. The exception to this occurred at 1520! A moderate wind blew at right angles to the ebbing current most of the afternoon which caused considerable agitation of the surface water, and may in part account for the high surface concentrations at 1420, 1520 and 1820. This, though, is not true of the high surface concentrations at 0820 and 0920 when the sky was heavily overcast and only a light wind was blowing.

There is fair similarity in the trends of the turbidity curve and the curve for maximum concentration of the 60-150 μ larvae, except at 1820 when the larval curve rose abruptly, and at 1120 when a broad fairly even distribution of the larvae occurred in the vertical column. Because of the muddy nature of the bottom in these waters the tidal currents carry much sediment into the water as they increase in velocity. These data for the straight hinge larvae appear to support only in part Perkin's research (T.

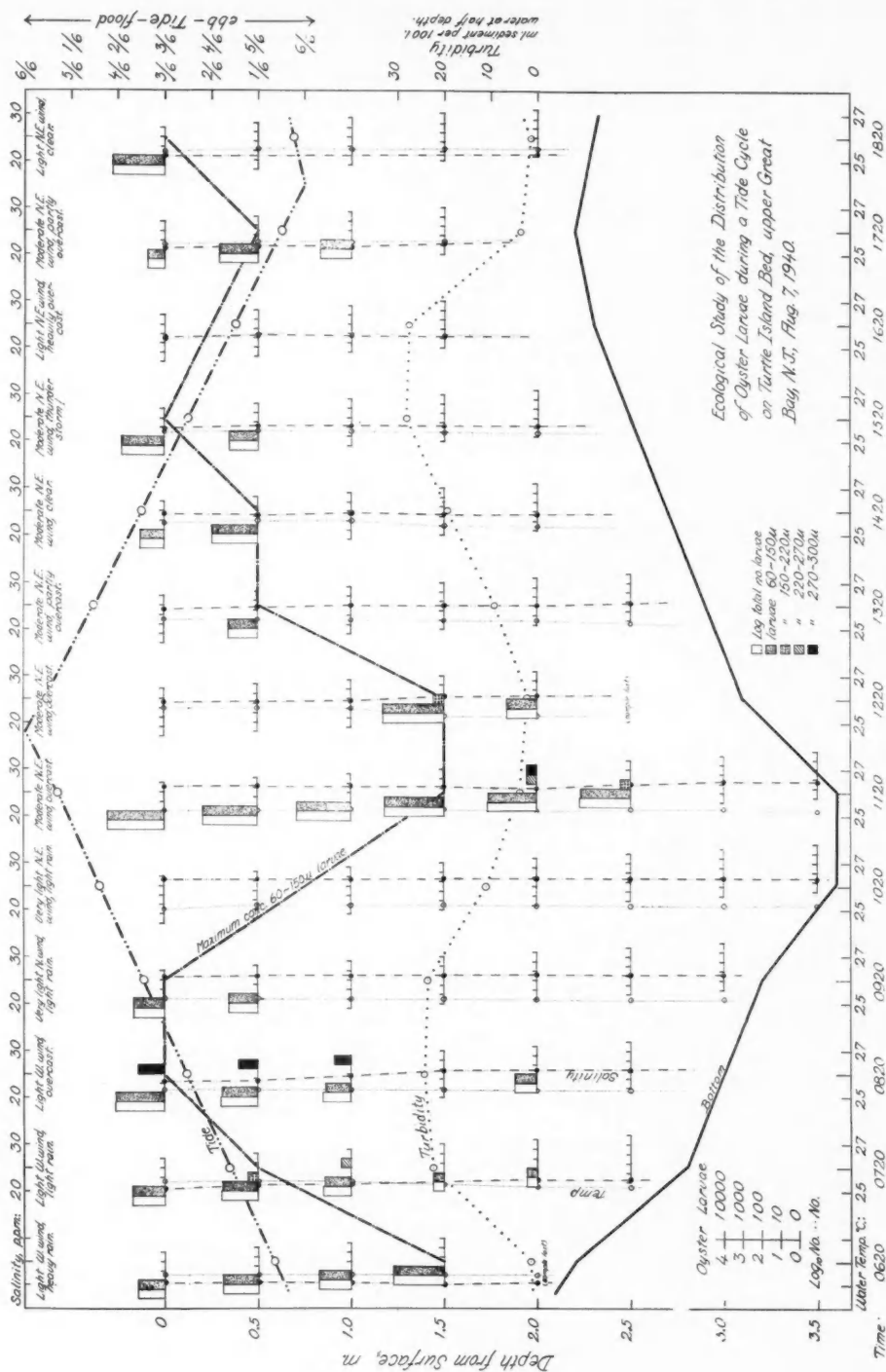


FIG. 4. The Turtle Island Bed tidal study.

Nelson and Perkins 1931, 1932) on the effect of current on larval distribution. For in addition to the apparent discrepancies at 1120 and 1820, it should be noted that the larvae are distributed in strata much nearer the surface than would be expected of inanimate microscopic bodies. T. Nelson (1931) explains this elevation of the larvae as a stimulation of the larvae to rise of their own accord over and above the strata reached by inert microscopic particles which may be carried passively by the current.

On July 22 a single vertical series of samples was pumped over the Turtle Island bed at 1000, at intervals of 1 meter, and at approximately 2/3 flood tide, which produced an unusual number of early and late umbo oyster larvae. A light northwest wind was blowing and the day was clear and hot. Temperature (26.2-25.5° C.) and salinity (23.1-26.5 ‰) varied uniformly from surface to bottom. The counts (fractionation) of early umbo larvae obtained from surface to bottom were: 2,400, 10,000, 6,750, 4,000 and 3,000; and those for late umbo larvae; 300, 1,500, 2,100, 300 and 300. According to the phase of the tide, this vertical column if placed with the data in Figure 4 would fall in the 1020 column, and whether coincidentally or not, the stratum of greatest early umbo larvae concentration in the July 22 column coincides with the theoretical one indicated in Figure 4 by the curve. The July 22 study again demonstrates the deeper distribution of the older stages of larvae and as compared with the similar study in Winter Creek the greater number of larvae found in the Bay.

Summer of 1947, Off Landing Creek

This season plankton samples were collected principally in water off Landing Creek along the south middle shore of Great Bay where conditions in the broad shallow portion of the Bay could be studied. The bottom here is composed of firm black mud, and tidal currents flow approximately southeast and northwest.

The period from February through June, with the exception of a warm period in the first half of April, was one of temperatures decidedly below normal; July was normal, and August one of the hottest since 1939, so that water temperatures were hitting peaks of 30° C. in the latter part of August in the Landing Creek area. Rainfall was below normal for the entire summer; salinities in the mid Great Bay area ranged from 18 to 31 ‰.

Oyster spawning was retarded considerably by the cold spring and early summer, so that the first large numbers of oyster larvae did not appear in the water until the end of July. Scattered spawnings continued throughout August with large numbers of straight hinge larvae appearing on the 18th and 23rd.

Thus by August 30 when the larvae were studied through the cycle of the tide there were present in the water a fair number of early and late umbo, mature, and eyed oyster larvae. On this day the motor boat was anchored about a half mile off the mouth of Landing Creek, which receives no fresh water except during heavy rainfall. Observations were begun at 0825 during the late flood slack and

continued through the flood slack in the evening. Forty-eight plankton samples were pumped, 4 per vertical series which were equally spaced between the surface sample (pumped at 0.1 meter) and the bottom sample which for the first time in these tidal studies was pumped directly off the bottom over the circular metal bottom disc described earlier. Temperature and salinity, because of the negligible differences generally observed in the vertical column, were determined for only one of the middle strata in each vertical series. The Secchi disc was used in recording the limits of visibility in the water, and meteorological observations were supplemented with readings of the quantity of light reflected from white paper. Tide levels were recorded on a portable tide gauge. It took 4 minutes to complete each of the bottom samples and 3 minutes for each of the others. For the first time, also, current velocity determinations were made to coincide with the depth of the water and phase of the tide at which plankton samples were pumped. The data for this tidal study are presented in Figure 5.

The current velocities were taken on September 11 at the same place and under similar tidal and wind conditions as those observed in the larval studies. On the ebb the maximum current velocity recorded was 19 cm./sec. at mid ebb (1130), and during this period the currents swept past the boat in a southeasterly direction, with only minor fluctuations in the surface strata from 0830 to 1030. During the flood (with the wind blowing behind it) the maximum velocity, 23 cm./sec., occurred at one-third flood in the different strata and ran northwest. On the early ebb the upper two-thirds of the vertical stream moved seaward with maximum velocity at about one-third depth; at the end of the ebb the deeper two-thirds of the stream accelerated and continued to move seaward while the upper third slackened. Finally on full flood the whole stream moved landward with maximum movement in the middle of the stream. Alternate moderate and strong south to south-southeast winds during the late ebb and the flood quickened the flood surface currents to the point where in some cases they moved faster than those in the axis of the stream.

Simultaneously with the taking of current velocities on September 11, serial vertical determinations of temperature and salinity were made through the tide cycle. Though these are not indicated in Figure 5, they have a bearing on the tidal study. Temperature differences were insignificant between surface and bottom. Only a slight halocline was present in the middle of the stream, especially during the early part of the ebb. It disappeared on the flood. The actual salinity readings, in parts per thousand, for the ebb tide vertical series starting with the surface (the time relates the figures to the proper vertical columns in Figure 5) were:

$\frac{1}{6}$ ebb (0930)	$\frac{1}{2}$ ebb (1130)	ebb slack (1400)
23.8	23.4	23.8
24.1	23.6	23.8
26.4	26.2	24.0
26.9	26.6	25.9

Ecological Study of the Distribution of Oyster Larvae through the Cycle of the Tide off Landing Creek, Great Bay, N.J., August 30, 1947

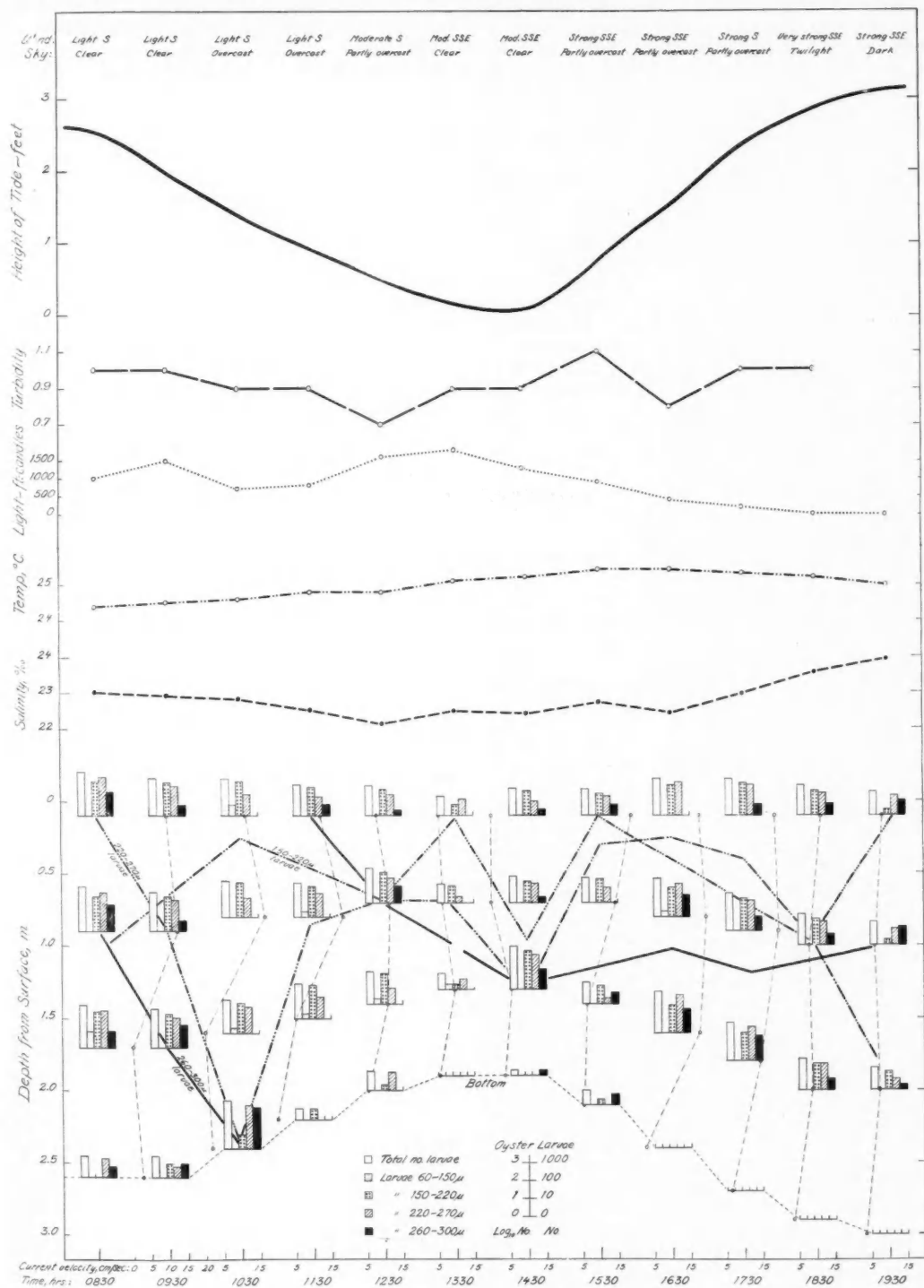


FIG. 5. The tidal study off Landing Creek.

The maximum number of total oyster larvae counted during the tidal study was 434 per 100 liters at 1030 on the bottom; of mature and eyed larvae, 182, at 1030, on the bottom; of late umbo larvae, 246, at 1030, also on the bottom; of early umbo larvae, 146, at 1430, at 1.3 meter depth; of straight hinge larvae, 8, at 0830, at 1.7 meter depth.

As compared with the previous tidal studies described in this paper, the one represented in Figure 5 discloses first a wide vertical and horizontal distribution of the larvae, and second the presence of a relatively large number of the older stages of the larvae. Of marked importance is the fact that significant numbers of larvae were found on the bottom during ebb and early flood and that they were completely absent there on the remainder of the flood. T. Nelson (1931) writes of a similar though isolated instance where Stauber pumped 700 eyed larvae per 100 liters of water from close to the bottom at ebb slack in Delaware Bay. Also to be noted, and supplementing similar observations in the previous studies herein reported, is the differential distribution of the different stages of the larvae through the cycle of the tide.

In analyzing the distribution of the various stages of the larvae in Figure 5, it is evident that the maximum concentration of early umbo larvae generally rose during the maximum current velocities of ebb and flood; but that on the whole, these larvae were fairly well distributed throughout the vertical columns. At 0930 the largest number of early umbo larvae were found at the level of maximum current velocity, then at 1030 rose above it and at 1130 and 1230 dropped below it. During the flood the maximum concentration remained above the level of the maximum current velocity.

In the course of the first 3 hours of ebb the largest swarms of late umbo, mature and eyed larvae dropped precipitously into the deeper levels and onto the bottom; this in spite of the greater current velocities in the upper third of the water. Toward late ebb a second grouping of these larvae appeared in the surface levels and then sank; they may have been stimulated to remain there by the slight halocline present during the ebb tide and by the agitation of the wind blowing against the current during the ebb, and then dropped as the halocline disappeared. During the flood these larvae ascended entirely off the bottom and tended to remain well distributed vertically in water which was well mixed both thermally and saliferously. Neither light nor turbidity, which was rather variable, seemed to correlate with the distribution of any of the larval stages.

SUMMARY OF THE TIDAL STUDIES

A survey of the actual number of the larvae encountered in the 4 tidal studies (see Table 2) emphasizes certain of the findings. For example, in the Lanoka Lagoon, Winter Creek, and Turtle Island Bed studies, more larvae of all stages were found on the flood than on the ebb. J. Nelson (1914 and 1917) reported similarly that at Tuckerton and at

Seullville (in relatively swift tidal currents) both stations agreed in giving a third less larvae on the receding tide than on the flood; though in Barnegat (where the tidal currents are less swift) he found the same number of larvae on the flood as on the ebb. In the present studies off Landing Creek, where currents are faster than in Lanoka Lagoon, more total larvae, both on and off the bottom, were found on the ebb than on the flood. It should be recalled that in the Lanoka Lagoon, Winter Creek and Turtle Island Bed observations, the sampling was started on the early flood, and off Landing Creek, on the early ebb. In this connection, that there is some loss of larvae from one tide to the next, should not be discounted. Just what the extent of loss of larvae under given conditions may be is not known. In any event the diminution from the large number of early stages found in the water to the few oyster spat counted on cultch later indicates a very high rate of larval mortality. Also, the first three tidal studies were carried out in relatively small tidal waterways in which on the flood the water sweeps upstream into smaller tributaries to spread over the marshes, where it is possible that considerable numbers of larvae were consumed by ciliary feeding and other animals. This fact along with the sinking of the older

TABLE 2. Summary of the Actual Number of Oyster Larvae Obtained in the Tide Cycle Studies.

Stage of the Tide		FLOOD				
Tide Cycle Study		Early stages	Late Umbos	Mature	Eyed	All stages
Lanoka Lagoon		2448	92	34	8	2582
Winter Creek		196	109	0	0	305
Turtle Island Bed		7316	8	8	48	7380
Off Landing Creek	Off the Bottom	610	654	130		1394
	On the Bottom	2	0	6		8

Stage of the Tide		EBB				
Tide Cycle Study		Early stages	Late Umbos	Mature	Eyed	All stages
Lanoka Lagoon		1128	54	42	0	1224
Winter Creek		88	55	0	0	143
Turtle Island Bed		2944	4	0	0	2948
Off Landing Creek	Off the Bottom	1028	698	102		1828
	On the Bottom	18	272	192		482

stages of the larvae on the ebb would explain in part the lesser number of larvae on the ebb than on the flood. On the other hand, in a larger body of water such as Great Bay (and possibly Barnegat Bay) it is quite possible, due to some horizontal circulation of the water, that the particular concentration of the larval swarm passing by the fixed sampling station on the ebb might be partly or entirely replaced by another concentration of the swarm in a different portion of the bay on the returning flood. Although larval loss through predation in lower Great Bay would still be high, it is assumed that it would not be as great as farther upbay since less of the larvae bearing water would be spreading thinly over the marshes and up the Mullica River and smaller tributaries. Thus off Landing Creek, in spite of the older larvae sinking to the bottom on the ebb, it is possible to account for the presence of more larvae on the ebb than on the flood.

In the Lanoka Lagoon and Turtle Island Bed studies no eyed larvae were found on the ebb, even though several were taken on the flood. In isolated vertical serial samplings other than the tidal studies in Lanoka Lagoon, eyed larvae were found only on the flood the entire summer. In the summers of 1939 and 1940 in upper Great Bay, although most of the eyed larvae were pumped on the flood tide, some appeared in the ebb tide: in the 2 summers, considering only the samples in which eyed larvae appeared, there was an average of approximately 8 eyed larvae per liters of water on the flood and 3 on the ebb. Off Landing Creek in the tidal study the mature and eyed larvae on the flood were taken predominantly in the water off the bottom, and were more numerous than on the ebb off the bottom. However on the ebb there were almost twice as many of these larvae directly on the bottom as off the bottom; and 32 times as many on the bottom on the ebb as on the flood.

DISCUSSION AND CONCLUSIONS

The results obtained in this ecological study of the movements of oyster larvae in native waters present a clearer and more exact picture of the actual vertical movements of the larvae with respect to the tides than has been known before, although they disclose but little more than has been revealed by previous observers of the influence exerted by the environmental factors on these movements.

The observations of J. Nelson, Gates, Stafford, Churchill, Gutsell, T. Nelson, Perkins, Prytherch, Loosanoff, Schaefer and Roughley that oyster larvae have a heterogeneous distribution in the water are amply confirmed. Also corroborated are the disclosures of T. Nelson and of Roughley that the different stages of the oyster larvae exhibit different vertical distributional patterns, the younger stages showing a more nearly uniform vertical disposition than the older stages which remain nearer the bottom. Further, and in accord with the results of T. Nelson, it has been shown that the younger stages of the larvae ebb and flow rather passively with the tide, tend-

ing to ascend into the surface layers in response to the swifter current velocities of mid flood and mid ebb and to remain in the vicinity of sharp haliclines when these are present. While the older stages tend to drop near or onto the bottom on the ebb and to rise into the water on the flood, thus making progress upbay, beyond that of passive conveyance by the ordinary run of the tides, possible. It is interesting to note in this connection that Gates as early as 1910 found oyster larvae upbay almost in fresh water and later Churchill and Gutsell observed that when large enough to set the oyster larvae were found some distance from the spawning ground—though they failed to connect this distribution with larval migration in the tidal streams. Elsey has shown that larvae move shoreward. And Prytherch also found that the larvae were most abundant in the lower strata of the water on the last of the ebb and nearer the surface on the early flood.

Prytherch's observation in Milford Harbor that "the majority of the larvae found were either a day or two old or nearly fully developed and ready to set," coincides in part with what has been shown to occur in New Jersey estuaries, and may be expanded as follows: Prytherch states that in Milford Harbor "the discharge of spawn occurs near or at the time of high water." As these early stages move more or less passively with the tidal currents, they are carried seaward away from the harbor by the tidal drift, the ebb running approximately 30 minutes longer than the flood during each cycle of the tide. Then as the larvae grow larger they probably exert independent vertical movements of their own, floating longer on the flood than on the ebb, and thus by the time of setting have returned toward the headwaters from whence they came, and often farther upstream, provided storms and adverse currents have not deflected their course.

It is difficult to explain why Prytherch found only a few larvae during mid flood and mid ebb whereas Loosanoff in the same waters in several instances found the larvae most numerous during the swiftest phase of the tide cycle. Loosanoff's observations, though, are in accord with our own in New Jersey and help to clarify Prytherch's findings in the Milford Harbor area. Though Loosanoff's other findings, i.e., no larvae in advanced stages of development near the bottom, do not agree with our New Jersey observations. It might well be that oyster larvae in the Milford Harbor area perform their migrations by means of a slightly different movement pattern which has so far evaded investigators. It is also possible that a more intensive sampling program is required to disclose the larval movements.

Also confirmed are the observations of Stafford, Churchill, Gutsell, Prytherch, Roughley and T. Nelson that the larvae tend to remain in definite lanes or areas. New is the discovery of relatively large numbers of mature and eyed larvae directly on the bottom on the ebbing tide. Although Prytherch found larvae on the bottom he makes no mention of what stages he found there nor what proportion of

the larvae were present on the bottom during the various phases of the tide cycle. It is assented with T. Nelson and Prytherch that oyster larvae are not passive planktonic forms, but it is not possible to concur with Prytherch's interpretation that the larvae by swimming only during the minimal tidal currents are able to remain and set on and near the spawning bed that produced them.

As to the influence exerted by certain environmental factors on larval movements, the studies herein reported substantiate T. Nelson's description of the part played by salinity and by current velocity in stimulating oyster larvae to move upbay. However, there yet remains much to be explained on such points as the minimum increment of salinity on the flood which when added to the effect of current velocity will be sufficient stimulus to cause the larvae to rise into the flood. The studies represented in Figure 5 present a situation where there is only a small change in salinity throughout the cycle of the tide, and yet the older larvae vividly demonstrate differential vertical movement on the ebb and on the flood tide.

Another factor which may bear investigating, in view of J. Nelson's records and those reported in this paper, is the effect of light, particularly between day and night, on larval behavior. And certainly simultaneous sampling of significant strata in the vertical column through tide cycles in many different fixed localities gives promise of more exact information on larval movements and a further knowledge of the part played by the environmental factors in larval behavior.

A further analysis of points 4 and 5 advanced by the Nelsons in support of their theory on larval migrations lends added support to this theory. Point 4 states that setting may occur far upstream from spawners, whereas seaward drift of the bay water over a period of 2 weeks would have carried inanimate particles far downstream from the parent beds. T. Nelson (1926) gives as an example the situation in Delaware Bay where some 30,000 acres of planted oysters 2 to 6 years old occur below the Southwest Line, and the river above this line for some 20 nautical miles (Fig. 4, T. Nelson 1947) contains the natural beds on which oyster seed are caught and held 1 or 2 years. Thus many of the larvae which set upon these natural beds must migrate "for miles upstream." A few calculations with the aid of Marmer (1926) and the 1947 *Current Tables, Atlantic Coast*, make Nelson's illustration even more striking: The average spring current velocity at strength of current just off the Southwest Line is approximately 1.8 knots, so that an average spring flood tide (starting, say, at the Southwest Line) would run upbay approximately 7 nautical miles; thus at most the larvae would be carried upstream only that distance . . . yet larvae set some 20 miles above this line.

Point 5 states that since in local estuaries the tide usually runs for a longer time on the ebb than on the flood, as a result of stream discharge, there is

produced a net drift which tends to carry all freely moving objects oceanwards. The fact that some of the larvae, even though carried seaward on the ebb, return to set far upbay would indicate that the larvae are actively swimming for longer periods during flood than on the ebb tide. Further hypothetical calculations with the aid of Marmer, the *Current Tables*, and Zeskind & LeLacheur (1926) lend credence to this phenomenon: Off the Southwest Line in Delaware Bay the average current velocity at strength of current is 1.5 knots. The average duration of flood is about 5.8 hours, and that for the ebb, about 6.6 hours. Thus on each succeeding ebb tide the larvae, provided they exert no independent movements of their own, would be carried about 0.8 mile downstream. And in the course of the average 14 day larval period, during some 27 ebb tides, and assuming a constant river discharge, the larvae would be carried seaward approximately 20 miles!

SUMMARY

1. A detailed survey of the literature pertinent to the movements of the larvae of oviparous oysters and the effect of such environmental factors as salinity, current velocity, temperature, light and pH on these movements is discussed.

2. The use of a sampling disc for pumping plankton samples off the bottom is introduced.

3. A more detailed description of larval movements with respect to the tide cycle than has been shown hitherto has been made possible by the collection of consecutive vertical serial samples at close intervals throughout the cycle of the tide.

4. Pen-and-ink drawings of the principal stages of oyster larvae, stressing the diagnostic external contours, and measurements of the various stages of the larvae are included.

5. A study of the distribution of oyster larvae through the tide cycle was made in Laroka Lagoon, Barnegat Bay; and in Winter Creek, Turtle Island Bed, and off Landing Creek, Great Bay over a period of four summers.

6. In the course of these tide cycle studies it was noted:

(a) that the larvae within the larval swarm itself are heterogeneously distributed in the water;

(b) that the larval swarms tend to remain in definite lanes or areas;

(c) that both salinity gradients and current velocity are influential in larval movements;

(d) that larvae occur in salinities as low as 3.1 ‰ and as high as 30.6 ‰;

(e) that more larvae are generally present on the flooding than on the ebbing tide;

(f) that the different stages of the larvae exhibit different vertical distributional patterns, the younger stages tend to drop near or onto the bottom on the ebb and to rise into the water on the flood;

(g) that the younger stages of the larvae ebb and flow rather passively with the tide; while the

older stages tend to drop near or onto the bottom on the ebb and to rise into the water on the flood;

(h) that, and not clearly demonstrated before, relatively large numbers of mature and eyed larvae may be present on the bottom during ebb tide.

7. Thus, in the light of these observations and those reviewed earlier, it may be concluded that the older larvae tend to migrate into the headwaters of estuaries to set beyond the distance made possible by tidal conveyance alone.

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RANGE CONDITION CLASSES OF NATIVE MIDWESTERN PASTURE: AN ECOLOGICAL ANALYSIS

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INTRODUCTION

Many tracts of native vegetation still remain in the western portion of that vast North American grassland known as True Prairie. Some are mowed annually for the crop of excellent forage, but far greater areas are now in native pasture (Weaver & Fitzpatrick 1932, 1934). One result of the long years of study of the grazed portion of this grassland was the recognition of the manner in which the prairie vegetation degenerates under continued grazing (Weaver & Hansen 1941). A second was the classification of the resulting pastures into several grades or range conditions, each based upon the composition of its vegetation (Weaver & Hansen 1941). Further ecological analysis of the different conditions of pastures was not made because of the 7 years of severe drought (1934-40). But after 8 good years for recovery of the greatly depleted grasslands, the present study was carried out in 1949.

The research was undertaken with a full knowledge that certain profound changes in prairie, which were also reflected in native pastures, had occurred both during and following the drought. There was a decrease in the amount of little bluestem (*Andropogon scoparius*)¹ which had been extremely abundant, and a resultant great increase in big bluestem (*A. furcatus*), formerly of much less abundance on upland. Marked local increases in prairie dropseed (*Sporobolus heterolepis*) and tall dropseed (*S. asper*) had also occurred. Decrease or disappearance of

certain forbs and great increases in others were apparent (Weaver & Albertson 1943). Finally, Kentucky bluegrass (*Poa pratensis*) had spread widely since the drought. From a predrought sprinkling of 3 to 5%, this sod-former now composed 15 to 20% of the vegetation of many isolated tracts of prairie, and was often even more abundant where these had been grazed (Weaver 1950).

The purpose of this study was to ascertain the percentage composition of the vegetation in several pastures of each grade or range condition as regards species of grasses and forbs. Also to compare the amount of vegetation available for forage during the growing season in the several range condition classes, and to express quantitatively the height to which the vegetation was utilized and the amount of mulch left on the soil.

CLASSES OF PRAIRIE PLANTS

The more abundant and important prairie plants have been separated into four classes by Weaver & Hansen (1941) according to the manner in which they respond to grazing. Their lists of species belonging to each class were compiled only after constantly checking the behavior of each species concerned in many pastures over a period of 12 years.

The first class includes grasses that decrease under grazing. In common usage species in this group are designated as decreasers. Here are included all of those grasses that are best-liked and most readily grazed by cattle. This includes about a dozen species. For brevity, only those that occurred abundantly in this study are listed.

¹The nomenclature of grasses follows Hitchcock's "Manual of the Grasses of the United States," that of other plants Britton and Brown's "Illustrated Flora."

DECREASERS

Hig bluestem	Needlegrass
<i>Andropogon furcatus</i>	<i>Stipa spartea</i>
Little bluestem	Plains muhly
<i>Andropogon scoparius</i>	<i>Muhlenbergia cuspidata</i>
Prairie dropseed	June grass
<i>Sporobolus heterolepis</i>	<i>Koeleria cristata</i>
Tall dropseed	Indian grass
<i>Sporobolus asper</i>	<i>Sorghastrum nutans</i>

A second class, decreasers among forbs, included practically all the legumes, but in this postdrought study only two in the list of 12 legumes and 32 other forbs (Weaver & Hansen 1941) were of sufficient abundance to warrant individual consideration. These are lead plant (*Amorpha canescens*) and many-flowered psoralea (*Psoralea floribunda*).

The third class is that of grasses that increase under grazing, and a fourth consists of forbs that respond in the same manner. The complete lists are quite long; the partial ones necessary in this study follow:

INCREASERS

GRASSES	FORBS
Kentucky bluegrass	Yarrow
<i>Poa pratensis</i>	<i>Achillea occidentalis</i> Raf.
Side-oats grama	Prairie cat's-foot
<i>Bouteloua curtipendula</i>	<i>Antennaria campestris</i>
Blue grama	Prairie mugwort
<i>Bouteloua gracilis</i>	<i>Artemisia gnapalodes</i>
Buffalo Grass	Many-flowered aster
<i>Buchloe dactyloides</i>	<i>Aster multiflorus</i>
Scribner's panic grass	Daisy fleabane
<i>Panicum scribnerianum</i>	<i>Erigeron ramosus</i>
Wilcox' panic grass	Pennyroyal
<i>Panicum wilcoxi</i>	<i>Hedeoma hispida</i>
Hairy grama	Yellow oxalis
<i>Bouteloua hirsuta</i>	<i>Xanthoxalis stricta</i>
Sedges	Smooth goldenrod
<i>Cyperaceae</i>	<i>Solidago glaberrima</i>
Rushes	Baldwin's ironweed
<i>Juncaceae</i>	<i>Vernonia baldwini</i>

While the first four classes deal with prairie species only, the fifth and sixth include grasses and forbs not common to prairie but weedy species that invade only after various prairie plants have been greatly weakened or have died.

INVADERS

GRASSES	FORBS
Sand dropseed	Annual ragweed
<i>Sporobolus cryptandrus</i>	<i>Ambrosia elatior</i>
Western wheat grass	Western ragweed
<i>Agropyron smithii</i>	<i>Ambrosia psilostachya</i>
Purple lovegrass	Flodman's thistle
<i>Eragrostis spectabilis</i>	<i>Cirsium flodmani</i>
Ticklegrass	Wavy-leaved thistle
<i>Agrostis hiemalis</i>	<i>Cirsium undulatum</i>
Little barley	Spotted spurge
<i>Hordeum pusillum</i>	<i>Euphorbia maculata</i>
Brome grasses	Snow-on-the-mountain
<i>Bromus spp.</i>	<i>Euphorbia marginata</i>
Turnbegrass	Gumweed
<i>Schedonnardus paniculatus</i>	<i>Grindelia squarrosa</i>
Annual dropseeds	Peppergrass
<i>Sporobolus vaginiflorus</i>	<i>Lepidium densiflorum</i>
<i>Sporobolus neglectus</i>	
Beard grass	Horseweed
<i>Paspalum stramineum</i>	<i>Leptilon canadense</i>
Six-weeks fescue	Pursh's plantain
<i>Festuca octoflora</i>	<i>Plantago purshii</i>
Crabgrass	Knotgrass
<i>Digitaria sanguinalis</i>	<i>Polygonum aviculare</i>
Stinkgrass	Dandelion
<i>Eragrostis cilianensis</i>	<i>Taraxacum officinale</i>
Canada bluegrass	Vervain
<i>Poa compressa</i>	<i>Verbena stricta</i>

PROCESS OF DEGENERATION OF PRAIRIE

Climax grassland, when grazed lightly or moderately, may retain essentially its natural composition over extremely long periods. It is only when grazing animals are circumscribed in their range by fences and when too large a population is thus confined that grazing and trampling become so excessive that the normal cover cannot be maintained.

The selection of grass types and preference for certain species by livestock is marked when forage is plentiful. Repeated partial removal of the most palatable grasses results in better growth of the remaining vegetation. In fact, if certain favored plants are grazed too early, too often, and too closely, they will disappear entirely. Less desirable species then receive more light and increased water as well as additional nutrients, which are normally used by the more palatable grasses. In consequence, they flourish and may actually increase, often with marked rapidity. Thus, during the early stages of grassland degeneration there is considerable shifting of the plant population, but this is entirely among the species which are normal components of native prairie.

As the hold of native species is weakened by continued pasturing or intense overgrazing, invaders come in. The great stability of natural grassland and the absence of weeds have been emphasized by Weaver & Flory (1934). But under pasturing many small, bare places appear. The bare areas invite invaders which once established furnish seed for a new population. Gradually the native grasses and forbs are partially or entirely replaced by invading species which are better adapted to close grazing and trampling. Nearly all of these are less productive, or less palatable, or both, than the original occupants. With the disappearance of most of the native population the prairies are far advanced on their way toward final disintegration (Fig. 1.).



FIG. 1. View from an excellent native pasture (right foreground, and opposite ungrazed prairie on the left) into a poor pasture, in right background. The light color is due to an abundance of ripened downy brome (*Bromus tectorum*). The dark bunches are ironweed (*Vernonia baldwini*). The left background was also prairie. The vegetation has only partly degenerated under grazing and the pasture is still in fair condition. Photo near Lincoln, 1944.

STAGES OF DEGENERATION²

Pastures in an excellent range condition are prairies that have not been misused. The forage usually exceeds the needs of the grazing animals. Grazing

² Much of this section has been taken from Weaver & Hansen (1941).

is very irregular or if regular is not too close so that 20 to 25 percent of the forage is left at the end of the growing season. Kentucky bluegrass, which usually becomes dry and bleached during the hot midsummer, has only a slight hold. Hence, during ordinary drought such pastures appear green and not dry. Favored areas are completely but not too often closely grazed, but others are undergrazed as is shown by old tufts and bunches and debris of former years. In fact irregular grazing is characteristic of this excellent range condition. Early stages of degeneration are not uniform but occur irregularly. Certain areas are favored by cattle as resting places during the heat of the day. Where no shade is to be found, ridges or flat uplands, where the cooling effect of wind may be felt, are used regularly. Here much trampling occurs and just beyond there is often rather close grazing. Such places early degenerate into bluegrass or shortgrass. Conversely, areas distant from water, especially where there are steep hills and deep ravines, and the steeper midslopes may not be grazed at all.

In general, bluegrass or blue grama and buffalo grass are beginning to increase. The amounts of these may be small in some pastures, but extensive in others, especially under big bluestem in ravines. Bluegrass is still local along pathways, flat ravine bottoms, and similar well-grazed places. Here all of the native bunch grasses have disappeared and the original occupants may constitute only half of the plant cover. Side-oats grama nearly always shows distinct increases. A few more or less inedible indicator species as ironweed, prairie cat's-foot, and many-flowered aster usually show an increase. Others, such as the very palatable ground plum (*Astragalus crassicaarpus*), many-flowered psoralea, upland sunflower (*Helianthus rigidus*) and round-headed bush clover (*Lespedeza capitata*), although frequent or abundant in prairie outside the fence, have almost entirely disappeared within the pasture. Although the shiftings are thus far among the native plant populations, a few invading weeds may occur sparingly to form a potential menace. Often, however, a striking feature of large areas in excellent range condition is the almost complete absence of weeds.

A second stage of degeneration of prairie is illustrated by good pastures or a good range condition class. Here because of longer or more intensive grazing, bluegrass or short grasses or alternating areas of these either equal or overbalance the usual prairie species and form the background or matrix of the vegetation. Usually the cattle graze as they travel about the pasture and there are few or no well-defined paths. Ravines have often gone over entirely to bluegrass. The original prairie species are clearly on the decline, although still abundant. The grass sod is still well intact since bluegrass or blue grama replaced the grazed-out native species. There is a moderate number of relict prairie forbs such as yarrow, many-flowered aster, and ironweed, all of which are unpalatable and not eaten, that are increasing. A moderate number of introduced weeds

not found in the prairie have appeared. Examples are vervain, thistles, and western ragweed. These are often confined to local, small and usually bared areas, but sometimes they are widely scattered. While many species of weeds may be present, only a few are abundant.

Native grasses are grazed more evenly and much closer to the soil than in excellent pastures. The size of the ungrazed places or areas grazed high varies greatly. They may cover the entire upper, middle, or lower slopes of the hill or form large patches on the level hilltop or on lowland. Conversely, they may be only a few feet in width. They vary with the season, amount of stocking, and other causes, but they characterize the good range condition. From May to midsummer forage production usually exceeds the amount the cattle consume. After midsummer, the reverse is true and the areas supporting well-liked grasses become more and more like a lawn. These places have been heavily invaded by bluegrass. The network of closely grazed patches increases at the expense of even the less palatable dropseeds which form roughs. But isolated bunches and groups of bunches of little bluestem, prairie dropseed, and tall dropseed show even the casual observer that this vegetation is still partly prairie. Closer study reveals an abundance of big bluestem, the weakened bunches of little bluestem, the near-depletion of needlegrass, etc., but also some excellent strongholds of various native grasses into which bluegrass is only slowly invading. In fact, one can see an almost equal balance between prairie grasses and prairie forbs on the one hand and the invasion of bluegrass (and sometimes blue grama) and certain weedy forbs on the other.

A third or fair pasture or range condition class maintains where overgrazing has occurred for a long period of years. Practically all of the native species have been replaced either by nearly pure stands of bluegrass or blue grama and buffalo grass or by a mixture of these species. In the best pastures the sod may be well intact but frequently it is broken. The ungrazed bluegrass foliage may reach a height of about 8 inches, but the flower stalks, which occur in great abundance, are often 5 to 8 inches taller. On the western edge of true prairie, as at Lincoln and westward, the tall and mid grasses are often almost completely replaced by the short ones, blue grama and buffalo grass. Sometimes the short grasses alternate in patches with bluegrass. Weeds are not plentiful in well-managed pastures but in poorer ones both perennial and annual weeds may become abundant. Ragweeds are among the most common invading forbs. Like many other plants, they occur in the dense sod, and the carpet of bluegrass or short grass is scarcely interrupted. Prairie forbs may be represented by some relict species but individuals are usually few in number. Often there are many square rods of bluegrass without a single prairie remnant. Banks bordering ravines where the slopes are steep or even moderately so are held longest by the native plants, since here bluegrass finds

invasion difficult. While most grasses long resist the impact of grazing, native forbs, with few exceptions, tend to disappear early. Both bluegrass and short grasses are sometimes so severely grazed that the stand becomes thin.

Poor pastures (poor range condition class) represent the final degeneration of prairie to a condition where weeds, including a host of annuals, compose much and sometimes most of the vegetation. Sometimes only the merest remnants of the original prairie species occur. Annual early grazing or overstocking or both have weakened the grasses so greatly that bluegrass and short grasses no longer furnish a continuous carpet of vegetation but occur in patches between which there is much bare soil or soil clothed only by invading weedy grasses and forbs. The deterioration has not taken place uniformly but has spread from the earlier centers of weed infestation. Unfortunately, these degenerate pastures are all too common.

THE AREAS STUDIED

The grasslands considered here occur within the western portion of the True Prairie association. They are located near Lincoln, Nebraska, in Lancaster County, which is about 70 miles east of the transitional area or ecotone that grades into mixed prairie. They consist of three groups or series of native pastures. Four different range condition classes are represented in each series. The individual pastures were selected simply by observing, as one walked through the pasture, the amount of decreasers and increasers among the native grasses and the degree of invasion of other grasses and forbs. One sufficiently acquainted with vegetation of true prairie to readily recognize the various species and approximate their relative abundance can readily determine the range condition class. An effort was made to widely space the series or groups of pastures but to select those for any one group as closely together as was convenient.

LOCATION AND SIZE

The first series of pastures was selected from range lands 7 to 9 miles northwest of the University of Nebraska and about 1 mile east of the highway to Raymond. This road skirts the broad flood plain of Oak Creek on the east at the foot of a long range of prairie-covered hills. The excellent pasture in this Raymond series is in Section 21, Township 11 N., Range 6 W. Like the others, it is enclosed by a barbed wire fence. It is about 55 acres in area. The good pasture, of approximately the same size, is located half a mile south of the first. A half-mile north of the excellent pasture is the one of fair range condition, with a nearly pure cover of bluegrass. It is about 70 acres in extent. The poor pasture lies half a mile west of the good one and is about 45 acres in area.

The second series is located 5 miles west of Lincoln, on similar rolling upland. All of the pastures are about 3 miles west of the Lincoln Municipal Air-

port, except that of fair condition which is located on similar terrain 3 miles west and 4 miles south of the preceding. The excellent pasture of this Airport series is in Section 12, Township 10 N., Range 6 E. It contains about 70 acres. The good pasture is located a mile southeast of this one and it is about 50 acres in extent. The poor pasture is approximately the same size as the good one and lies one-fourth mile southeast of it. The pasture in fair condition to the southwest is in Section 33, Township 9 N., Range 5 E. Its area is about 60 acres.

The third series of pastures was selected on rolling range lands about 18 miles southwest of Lincoln and 4 miles southwest of Denton. All four range condition classes occur within a distance of 2 miles. The excellent pasture consists of about 200 acres. It is in Section 4, Township 9 N., Range 5 E. Only about 60 acres of this pasture were sampled. The good pasture contains about 220 acres and lies about one-half mile south of the excellent one. About 60 acres of it were sampled. The fair pasture is located about three-fourths mile north and west of the excellent one; two adjacent areas, each of about 25 acres, were sampled in this study. The poor pasture lies across the road, east and a half-mile north of the excellent one. Like most poor pastures, it has a smaller area than those of higher grade.

TOPOGRAPHY, WATER, AND SOIL

The topography in all twelve pastures is that of moderately rolling upland. Each pasture has one complete hill or ridge with slopes of various exposures, some level upland and at least small amounts of nearly level land along the ravines (Fig. 2). The general elevation is between 1,200 and 1,400 feet. In places ravines were 10 to 15 feet deep and had steep slopes, which were mostly covered with vege-

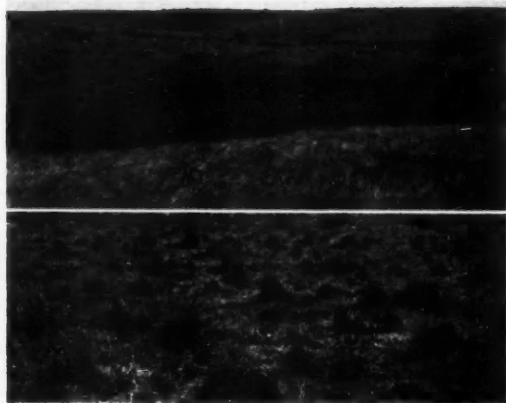


FIG. 2. (Above) Typical hilly land clothed mostly with bluestems (*Andropogon*), dropseeds (*Sporobolus*), and Kentucky bluegrass (*Poa pratensis*). The prairie is annually grazed from early spring until late fall. (Below) Detailed view in an excellent pasture. The bunches are nearly all little bluestem (*Andropogon scoparius*) and the lower vegetation is mostly big bluestem (*A. furcatus*). Forbs are few and very little bluegrass is present. The pasture is moderately grazed.

tation. Above these slopes, more gentle ones prevailed. They varied from 2-5 to 7-10% over the greatest expanse of the hills, some of which had gently sloping to nearly level tops. The hilltops are between 50 and 130 feet above the ravines. Although much runoff water may be carried down the ravines during heavy rains, nearly all are dry, except for a few days after a rain.

Enough water is impounded in spring to last during the grazing season by dams which have been placed across some of the larger ravines. Water for stock is obtained in some pastures from these artificial ponds. Often this supply is supplemented or entirely replaced by water from wells pumped by windmills into large steel tanks. Distance of any part of a pasture to an abundant supply of water was not great. Usually it did not exceed three-fourths of a mile and in only one pasture was it a mile.

The dominant type of soil is Carrington loam or silty clay loam. This is a very productive soil which occurs widely in eastern Nebraska and in Iowa. Smaller areas of other soil types occur but resulting differences in growth of native species are usually small. On Steinauer loam vegetation was poorer, on Judson silt loam of well-drained lowlands it was much better than on Carrington. But Carrington was the major soil type in all the pastures studied.

The topsoil or A horizon of Carrington silt loam is often 10 to 12 inches thick and the subsoil or B horizon 18 to 24 inches. In some places these soil horizons, which constitute the solum, appear to have developed from thin layers of loess, but in other places from glacial till. Parent material of the C horizon is often glacial till. It contains small pebbles and grit mixed with clay and silt in greatly varying proportions. Although the calcium carbonate in these zonal Prairie soils has been leached from the solum, and no free lime may be found to a depth of 5 feet, the pH is usually about 6.5. These dark colored soils are mostly fine granular silt loams, very receptive to water when clothed with grass. The lighter colored, often brownish-yellow parent material is many feet in depth. The precipitation, about 27.5 inches annually, moistens the soil deeply. Both surface and internal drainage are good.

This soil type supports vegetation which may produce 1.5 tons of hay per acre. The bluestem grasses extend their roots 4 to 6 feet deep on upland, and various forbs, including legumes, much deeper (Weaver 1919, 1950a; Weaver & Darland 1949). Root depth, like that of percolating water, is nowhere hindered by layers of rock, although buried glacial rocks may occur.

VEGETATION

The excellent pastures were all former prairies that had been mowed annually for hay. They differ but little from typical climax true prairie. A wide variety of native prairie grasses occurred, and their distribution into local, nearly pure communities, alternates, or mixed stands had not yet been much modi-

fied. Usually big bluestem was the most widely distributed over lowlands, lower hillsides, and often on level hilltops, despite the fact that bunches of little bluestem were far more conspicuous. The increased dominance of big bluestem, resulting from decreased amounts of little bluestem during the great drought, was still pronounced in each of the three excellent pastures.

EXCELLENT PASTURES

For clearness of presentation, conditions in the excellent pasture near Raymond will be noted briefly and then differences between it and the others of this class will be pointed out (Fig. 3). The prairie dropseed type was pronounced on the hilltops and slopes. In some places, the large, very definite bunches, spaced 6 to 14 inches apart, often formed 90 percent of the vegetation. In past years there had been little grazing here. Such stands of dense ungrazed or little grazed vegetation, even if in small patches, are designated as roughs. Since the annual crop of forage is not removed, they stand out in sharp contrast with the other vegetation (Fig. 4). Frequently prairie dropseed was rather equally intermixed with bunches of tall dropseed; here other grasses, except big bluestem, were absent or few. In still other places each of the dropseeds formed a small percentage of the vegetation which was mostly bluestems.

The prairie forbs occurred in their usual post-drought abundance. As a whole the chief societies were those of lead plant, many-flowered psoralea, many-flowered aster, and smooth goldenrod, but a great variety of species occurred.

Bluegrass was almost absent where the dropseeds grew thickly. It was abundant along the ravines where big bluestem had been nearly grazed out. Almost pure local stands bordered the larger valley where the best-liked grass, big bluestem, had been largely replaced by it.

The excellent pasture in the Airport series was characterized chiefly by the bluestems. There was



FIG. 3. Typical view in the excellent pasture near Raymond. The foreground is the upper portion of a ravine where the bunches of little bluestem have mostly been grazed, some closely. Bluegrass is spreading here, but farther up the hillside nearly all the vegetation is composed of prairie grasses and forbs.

almost a uniform mixture of the two species which together formed more than two-thirds of the vegetation. The third great dominant, prairie dropseed, occurred in less abundance. There was very little tall dropseed. Grazing had been far more uniform,

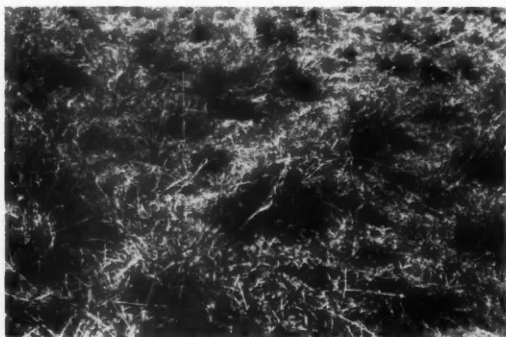


FIG. 4. Portion of a large rough in the excellent pasture at Raymond. The bunches are almost entirely tall dropseed (*Sporobolus asper*). Photo in early spring of 1949. Only the tops of the bunches had been grazed back to about 18 inches the preceding season. There was only a small amount of grazing of the sparse big bluestem (*Andropogon furcatus*) which grew between the bunches. Bluegrass occurred very sparingly.



FIG. 5. Two of the seven most abundant forbs of upland prairie, showing their predrought societies. Upper one is lead plant (*Amorpha canescens*). It is really a half-shrub but behaves as a forb under annual mowing. The lower one is silvery psoralea (*Psoralea argophylla*). It is smaller in stature but usually far more abundant and widely distributed than *P. floribunda*.

though still selective, than in the Raymond pasture. Roughs were fewer but in them the grasses were often grazed about 8 inches high. Lead plant was again the chief forb but *Psoralea floribunda* was also very abundant (Fig. 5).

At Denton big bluestem and little bluestem dominated. Prairie dropseed and tall dropseed occurred sparingly. Much less bluegrass occurred here than in either of the preceding pastures. This indicated somewhat less usage.

GOOD PASTURES

Upon entering a good pasture one can readily see that a large part of the native vegetation common to excellent pastures is missing. Areas of rather closely and more or less uniformly grazed vegetation alternate with other more or less continuous stands that have been grazed high or perhaps not at all (Fig. 6).

An outstanding feature in the good pasture at Raymond was the absence of ungrazed bunches of little bluestem. Nearly all had been grazed repeatedly and often close to the soil surface. The former patches of ungrazed prairie dropseed and tall dropseed (roughs) were relatively few and small. Some grazing had occurred in all of them where the cattle sought and ate the bluestems. In nearly all, some bluegrass occurred. These roughs alternated with uniformly and closely grazed areas of bluegrass, which maintained a good mixture of big bluestem. Bluegrass appeared to furnish nearly half of the vegetation. Often only single bunches of prairie dropseed remained where they once grew thickly. Invading grasses were few. Most prairie forbs had decreased, especially the lead plant. Ironweed, yarrow, prairie sage, many-flowered aster, and smooth goldenrod, all little disturbed by cattle, formed the chief societies. A few invaders were scattered widely but thinly, because of the almost continuous sod.



FIG. 6. General view on the south slope of the large hill in the good pasture of the Raymond series. Note that nearly all of the bunches of little bluestem and prairie dropseed have been grazed. Big bluestem is plentiful but has been eaten back uniformly. Bluegrass is abundant and it alone occupies many of the patches where all of the bunch grasses have been grazed out. Photo in May, 1949.

In the good pasture of the Airport series big bluestem and Kentucky bluegrass appeared to be most abundant, with little bluestem and side-oats grama occurring in somewhat smaller amounts. Bluegrass and side-oats grama were the chief grasses that had increased under the several years of grazing. Roughs were not abundant. Ironweed, yarrow, and prairie cat's-foot had increased greatly. Western ragweed, thistles and vervain were the chief invading forbs.

In the good pasture at Denton, total bluestems were somewhat less abundant than at the Airport. They, with tall dropseed, seemed to nearly balance the bluegrass in amount in the area of apparent bluegrass sod. The bunches of little bluestem had been almost cleared from some locations by repeated grazing. Mostly they were plentiful, and sometimes they formed roughs (Fig. 7).



FIG. 7. Detail of a small rough in the good pasture in the Denton series. The bunches are little bluestem and tall dropseed. They are surrounded by bluegrass sod which contains much big bluestem and remnants of little bluestem and other prairie grasses. These roughs will disappear when forage becomes less plentiful.

FAIR PASTURES

The pasture selected at Raymond represented a rather high type of the fair range condition. Some big bluestem was still sprinkled throughout much of the ever-present bluegrass sod, although little bluestem was rare. There was no needlegrass, prairie dropseed, or tall dropseed. Practically all of the prairie grasses and edible forbs were gone. Ironweed had spread from its prairie home in lowlands and ravines over the uplands and often developed bunches or clumps instead of one or a few stems as in prairie. It was one of the most conspicuous among several species of weeds. A few other prairie forbs had increased greatly to form societies, especially those mentioned as common in the pasture of the next higher grade. Invading grasses were few, but they would spread rapidly and widely if grazing and trampling weakened and finally opened the cover of bluegrass sod.

The fair pasture in the Airport series was likewise dominated throughout by bluegrass (Fig. 8). The invading sand dropseed was fairly common. Of relict prairie grasses, big bluestem was widely scattered in

small amounts. Only a trace of little bluestem was found, while the dropseeds and various other prairie grasses had completely disappeared. A few native forbs had increased considerably. Among these ironweed was the most important. Most prairie forbs, including all the legumes, except the inedible false indigo (*Baptisia bracteata*) had been grazed out. Thistles and vervain were moderately abundant but were greatly exceeded in amount by western ragweed.



FIG. 8. The fair pasture on a north hillside in the Airport series. The vegetation is about two-thirds bluegrass. Practically all decreaseers, both grasses and forbs, have been grazed out. Ironweed (*Vernonia baldwini*), dark in color, had spread widely. Western ragweed (*Ambrosia psilostachya*) is the most abundant invading forb. July 15, 1949.

At Denton the fair pasture consisted of extensive stands of blue grama and minor ones of buffalo grass. The patches of bluegrass sod were small and relatively few. Big bluestem and some little bluestem still survived in the interspaces between mats or in openings in the sod. Some sand dropseed had invaded the bared areas on the margins of the clumps and mats. Yarrow, sage, and many-flowered aster, all survivors of prairie vegetation, were common in the mats of short grass. Western ragweed was by far the most important forb. Degeneration of prairie to short grass, like its replacement by bluegrass, greatly reduces the amount of forage and excludes many of the best-liked grasses and forbs.

POOR PASTURES

The poor pasture in the Airport series, like all others, appeared very weedy and the vegetation varied greatly in height. There was much bare ground almost everywhere. Only small patches of bluegrass, blue grama, or buffalo grass remained and the sod was thickly populated with weeds (Fig. 9). Only a few other perennial grasses were found. Invading sand dropseed was the most abundant perennial grass while side-oats grama ranked second. Prairie cat's-foot occurred in very large patches, but yarrow and ironweed were the chief native forbs that had greatly increased. There were numerous invading weedy grasses among which the annual dropseed was by far the most abundant. The perennial ragweed ranked first in abundance among invading weeds and the thickest patches nearly obscured all other vegetation. Next in abundance was gumweed which, like the ragweeds, is of little or no forage



FIG. 9. A poor pasture everywhere infested with ironweed. No prairie relicts occur. It has resulted from overstocking a good bluegrass pasture. The weeds shade out the bluegrass; total production of forage is low. This pasture was not used in this study.



FIG. 10. Poor pasture in the Airport series. A dense stand of gumweed (*Grindelia squarrosa*) in the foreground shades out almost all the grasses. Patches of sand dropseed (*Sporobolus cryptandrus*), annual dropseed (*S. vaginiflorus*), and blue grama (*Bouteloua gracilis*) occur on the hillside. There are many kinds of weeds and there is much bare soil.

value. The vervain was widely distributed. Ironweed had aggregated into clumps and its wide distribution showed plainly that this was indeed an old pasture (Fig. 10).

The poor pasture at Denton differed chiefly in having considerable bluegrass even though the sod was broken up into small patches which alternated with weed-infested bare soil. Other prairie grasses were rare. The kinds and abundance of invading weedy grasses and invading forbs was impressive. In all these pastures the livestock was poor. There was an excessive amount of trampling as the herd wandered about searching for forage.

METHODS

Vegetation in each of the 12 pastures was sampled in numerous, well distributed, square-foot areas. The pastures, including the portions used in the very large ones, were nearly square or broadly rectangular. Topographic conditions were so similar in all of them that each had one main hill with various slope exposures, level hilltop, and some nearly level lowland. Two lines were run and permanently marked

in such a manner that each crossed the pasture in a diagonal direction; one line intersected the other near the center of the pasture and somewhere on the top of the hill. Sampling along the lines was at random and usually at intervals of 15 to 20 paces. The general plan was the same in all, even in the smallest pastures the samples were 12 paces apart. Where atypical places occurred, as slough grass and coarse sedges in deep ravines, bared banks, trails, etc., no samples were taken. Of the 150 areas sampled in each pasture, 50 were taken in June, 50 in July, and the remainder in August. The July samples were along the same lines as those made in June, only the starting point was several paces back of the first one. Hence all the samples were taken between those of June. Likewise in August the starting point was a few paces beyond that of June and again all the samples were between those formerly taken.

The quadrat frame consisted of a strip of steel and was so constructed as to enclose three sides of a square foot. The strip was one-eighth inch thick and the frame half an inch high. The open side permitted the frame to be slid on the soil and through the vegetation of the selected area. The fourth side was then placed across the open end and fitted into slots to hold it in place. Location of the sample was at random and was determined by the position of the shoe of the investigator when, without observing the ground, the last step was taken. Two men cooperated in securing data. This not only facilitated the study but was an effectual check upon the observations.

After placing the quadrat frame, the square foot was divided into four equal areas by laying long steel quadrat pins across the frame in two directions. The pins rested in shallow grooves made by filing the top of the frame. The presence of all species was then recorded. Next the basal area occupied by the vegetation 1.5 inches above the soil surface was estimated in each part of the quadrat and the average of the four numbers was recorded. Percentage composition of the vegetation was next ascertained. In doing this, the total vegetation, regardless of its amount, was considered as unity or 100%. Usually two or three grasses formed the bulk of the vegetation, the total of their separate percentages of composition amounting to 80-90. The percent of each species was based upon the part of the total basal area (now considered as 100%) that each furnished. Basal area of forbs was usually very small and it was not recorded unless it exceeded 5%, since their amount was later ascertained on the basis of dry weight. Likewise the basal area of every grass or sedge was recorded only if it furnished at least 5% of the total basal area. Thus, the species in small amounts were ignored and the 100% basal area of the vegetation was divided among the remaining abundant species.

Whether or not the sample had been grazed was next recorded together with height of grazing. The plants were then cut selectively and bagged, air

dried, and weighed in 6 separate groups. These were grasses that decreased under grazing, those that increased, and those that invaded. Three similar groups were used for forbs. In this manner the amount of unconsumed vegetation at the time of sampling was obtained.

Finally, the percentage of bare ground, if any, was recorded. In each fifth sample, the soil mulch was estimated and recorded as belonging to one of five classes; 0 or none, 1 or light, 2 or moderate, 3 or heavy, and 4 or excessive. The mulch from each fifth sample in each pasture was collected, air-dried, and weighed.

Each individual sample was classified on a percentage basis as grass decreaseers, increaseers, and invaders, and forbs. These figures of percentage were transformed to angles so that the data could be treated statistically. Such treatment of the data presented in this study has shown that the sampling was adequate for all pastures of each range condition class in the three series.

COMPARISON OF RANGE CONDITION CLASSES

Percentage composition of the vegetation is the most satisfactory basis for classifying ranges in the midwestern United States and the one now most widely used. Consequently it will be given first consideration. In a study of the pastures, examination of each group required many days. Hence, it was decided that more uniform results might be obtained by extending the sampling in each pasture throughout the summer. This proved to be very satisfactory

TABLE 1. Average percentage of the vegetation in each pasture of each range condition class furnished in each month's samples by big bluestem, bluegrass, and sand dropseed, respectively. The Raymond, Airport, and Denton series are indicated, in order, by R, A, and D. At the Denton fair pasture the percentages are for blue grama and not for bluegrass.

Class	Month	BIG BLUESTEM			BLUEGRASS			SAND DROPSIED		
		R	A	D	R	A	D	R	A	D
Exc.	June.....	14.7	29.9	33.5	33.2	15.7	6.2	0.6
	July.....	16.2	27.3	27.0	23.9	16.2	5.7	0.7
	August.....	16.5	27.8	30.0	25.4	10.5	8.8	0.5
	Ave.....	15.8	28.3	30.2	27.5	14.1	6.9	0.6
Good	June.....	10.7	26.5	9.5	44.1	36.3	43.9	2.5	2.4	0.1
	July.....	10.2	20.8	8.8	36.0	41.8	45.0	2.6	1.7	0.5
	August.....	11.9	24.5	9.0	46.0	35.0	34.1	1.8	1.7	0.7
	Ave.....	10.9	23.9	9.1	42.0	37.7	41.0	2.3	1.9	0.4
Fair	June.....	5.0	2.6	2.2	84.5	72.4	82.1	1.1	10.5	1.0
	July.....	2.5	1.7	2.0	85.6	65.6	82.4	0.9	11.7	2.6
	August.....	3.2	3.8	1.8	80.9	64.0	85.4	1.9	6.7	1.6
	Ave.....	3.6	2.7	2.0	83.7	67.3	83.3	1.3	9.6	1.7
Poor	June.....	...	4.7	...	38.1	1.0	24.8	11.0	8.7	5.2
	July.....	...	5.5	...	46.7	1.1	25.2	9.9	9.5	9.0
	August.....	...	4.0	1.2	49.5	...	22.8	6.4	11.5	3.4
	Ave.....	...	4.7	0.4	44.8	0.7	24.3	9.1	9.9	5.9

in practice and resulted in a better understanding of the vegetation ecologically.

The three individual pastures in each range condition class will now be compared. In this manner a definite idea may be obtained regarding the composition of the vegetation in each, and how little or how greatly it varied within each class. This procedure also permits an exact comparison of how the decreaseers, increaseers, and invaders vary in number and amount in the excellent, good, fair, and poor pastures.

In tabulating the data, big bluestem is placed first in the list of decreaseers since this is its usual rank in practically all the pastures. Bluegrass was by far the most abundant increaseer, and sand dropseed ranked highest among invading perennial grasses. The percentage of the vegetation which each of these species composed in each pasture from samples taken in June, July, and August, respectively, is shown in Table 1. The percentage composition of these grasses each month in each pasture is remarkably similar. Hereafter, the average percentage of composition, and not those percentages obtained each month, will be used in considering the part each of these and other species furnish in the total amount of vegetation.

EXCELLENT RANGE CONDITION

The number of species of grasses in excellent pastures was small. This is because those that did not furnish 5% of the vegetation in at least one sampling area were omitted. Small amounts in the samples also accounts for the low percentages of composition of 3 of the 7 species of decreaseers (Table 2). There are also only 7 species of increaseers and 4 of invaders. One of these, purple lovegrass, is "a perennial species of a somewhat weedy nature. It is found widely distributed over the prairie but rarely in abundance" (Weaver & Fitzpatrick 1934). It has increased somewhat since the drought but usually furnishes only a fraction of 1% of the vegetation. Since it is later included with invaders where yields are considered, it will be maintained here also in the group of invaders.

The bluestems rank high in the Airport pasture but even higher at Denton (Table 2). Each formed an average of one-fourth of the total vegetation. The great amount of bluestems at Denton compensates for the small amount of the third most abundant dominant, prairie dropseed. Amount of tall dropseed is not great, only 3 to 5% in each of the three pastures. Other decreaseers are of little importance. Total decreaseers for the three pastures in order were 55, 69, and 75%, and on an average decreaseers furnished two-thirds of the total basal area of the vegetation.

There was very little bluegrass (about 7%) at Denton where bluestems were most abundant; twice as much occurred at the Airport, and four times as much (27.5%) at Raymond. Side-oats grama ranked second and fairly high, about 11 to 15%, in all pastures. It furnished on an average 13% of the

TABLE 2. Percentage composition of the vegetation in excellent pastures at Raymond, Airport, and Denton. The figures in each column are averages of 150 samples taken during the summer.

Species	Raymond	Airport	Denton	Ave.
DECREASERS				
Big bluestem.....	15.8	28.3	30.2	24.8
Little bluestem.....	12.9	20.8	41.2	25.0
Prairie dropseed.....	20.1	14.7	0.3	11.7
Tall dropseed.....	5.2	5.2	3.0	4.5
Needlegrass.....	0.9	...	0.1	0.3
Plains muhly.....	0.1	0.2	0.3	0.2
June grass.....	...	0.1	0.3	0.1
Total.....	(55.0)	(69.3)	(75.4)	(66.6)
INCREASERS				
Kentucky bluegrass...	27.5	14.1	6.9	16.2
Side-oats grama.....	14.7	13.8	10.8	13.1
Blue grama.....	0.7	0.2
Scribner's & Wilcox ¹
Panic grass.....	...	0.3	0.2	0.2
Sedges.....	...	0.2	0.5	0.2
Rushes.....	0.2	0.2	1.3	0.6
Total.....	(43.1)	(28.6)	(19.7)	(30.5)
INVADERS				
Sand dropseed.....	0.6	0.2
Western wheat grass...	1.0	0.1	...	0.4
Purple lovegrass.....	0.1	1.4	2.8	1.4
Ticklegrass.....	0.3	0.1
Total.....	(1.1)	(1.5)	(3.7)	(2.1)
Forbs.....	0.8	0.6	1.2	0.9
Grand Total.....	100	100	100	100.1

vegetation. Other increasers occurred in such small amounts that the average total was 30%. Of the sedges, *Carex pennsylvanica* was the most abundant in all pastures.

No invading species contributed more than an average of about 1%, and the total was only 2. The very small amount of invaders is characteristic of prairies and pastures in excellent condition.

GOOD RANGE CONDITION

A second group consisting of one good pasture from each series, revealed some marked changes. These are almost entirely due to a loss in percentage composition of about half the amount previously furnished by the decreasers, and a corresponding gain by increasers to twice their former abundance. Invaders composed a very small part of the vegetation, since the sod was still intact almost everywhere (Table 3).

Big bluestem exceeded little bluestem in amount in the Airport pasture, but the reverse was true at Raymond and Denton. Decrease in big bluestem was consistent in all three good pastures. There was more little bluestem in the good pasture at Raymond (probably because of less dropseed) than in the excellent pasture. Despite irregularities in individual

TABLE 3. Percentage composition of the vegetation in the good pastures at Raymond, Airport, and Denton. The figures in each column are averages from 150 samples taken during the summer.

Species	Raymond	Airport	Denton	Ave.
DECREASERS				
Big bluestem.....	10.9	23.9	9.1	14.6
Little bluestem.....	18.8	10.0	13.8	14.2
Prairie dropseed.....	5.6	...	0.4	2.0
Tall dropseed.....	3.0	0.1	5.8	3.0
Needlegrass.....
Plains muhly.....	0.6	0.2
June grass.....	0.4	0.1
Indian grass.....	0.3	0.1
Total.....	(39.3)	(34.0)	(29.4)	(34.2)
INCREASERS				
Kentucky bluegrass...	42.0	37.7	41.0	40.2
Side-oats grama.....	10.8	16.5	16.0	14.4
Blue grama.....	3.9	3.5	1.9	3.1
Scribner's & Wilcox ¹
Panic grass.....	...	0.1	0.3	0.1
Hairy grama.....	4.7	1.6
Sedges.....	...	0.8	0.1	0.3
Rushes.....	...	0.4	2.2	0.9
Total.....	(56.7)	(59.0)	(66.2)	(60.6)
INVADERS				
Sand dropseed.....	2.3	1.9	0.4	1.5
Western wheat grass...
Purple lovegrass.....	...	0.5	0.4	0.3
Ticklegrass.....
Little barley.....	...	0.6	...	0.2
Brome grasses.....	...	1.5	...	0.5
Tumblegrass.....	...	0.3	...	0.1
Annual dropseeds.....	1.1	0.4
Bead grass.....	0.3	0.1
Total.....	(2.3)	(4.8)	(2.2)	(3.1)
Forbs.....	1.7	2.2	2.2	2.0
Grand Total.....	100	100	100	99.9

pastures, the average decrease of the two species was the same. Each now composed about 14.5%. There was much less prairie dropseed, if any, in each good pasture. Average decrease was from almost 12 to 2%. Other changes among decreasers were insignificant.

Bluegrass had increased from 28 to 42% at Raymond, from 14 to 38 at the Airport, and from 7 to 41% at Denton. It alone furnished an average of 40% of the vegetation. Average increase in the total amount of side-oats grama from excellent to good pasture was only 1%. Blue grama occurred in all of the good pastures but in only one in excellent condition. Amounts, however, were small, about 3%. Since amounts of other increasers as well as invaders and forbs were also small, the gains are almost entirely due to the spreading of bluegrass. It now occurred in 92% of all the sampling areas in good pastures. Many of its competitors were reduced in vigor. Unless grazing pressure is reduced in these

good pastures, drastic changes will result, such as those which had already occurred in pastures designated as fair.

FAIR RANGE CONDITION

Enormous gains of increasers (from an average percentage of 61 to 88) and great losses of decreasers (from an average percentage of 34 to 4) characterized the change from good pastures to the fair ones. Even invading grasses had doubled in amount (Table 4). Big bluestem was everywhere reduced to about 2 to 4%. Amounts of living little bluestem were less, although dead crowns were not uncommon. Only remnants of dropseed were found, and other decreasers had died. Amount of bluegrass was greatest at Raymond (84%). In the Denton pasture blue grama played the usual role of bluegrass and will be considered in its place as the leading increaser. Here it formed the matrix of the vegetation to the extent of 82%; a small percent of buffalo grass is included in the number in Table 4. The smallest amount of

TABLE 4. Percentage composition of the vegetation in the fair pastures at Raymond, Airport, and Denton. The figures in each column are averages of 150 samples taken during the summer.

Species	Raymond	Airport	Denton	Ave.
DECREASERS				
Big bluestem	3.6	2.7	2.0	2.8
Little bluestem	0.5	1.9	0.5	1.0
Prairie dropseed
Tall dropseed	0.2	...	0.2	0.1
Needlegrass
Plains muhly
June grass
Indian grass
Total	(4.3)	(4.6)	(2.7)	(3.9)
INCREASERS				
Kentucky bluegrass	83.7	67.3	0.8	50.6
Side-oats grama	5.3	6.6	6.7	6.2
Blue grama	1.8	2.4	83.3	29.2
Scribner's & Wilcox'
Panic grass	0.3	1.2	...	0.5
Hairy grama
Sedges	1.8	2.1	0.6	1.5
Rushes	...	0.1
Total	(92.9)	(79.7)	(91.4)	(88.0)
INVADERS				
Sand dropseed	1.3	9.6	1.7	4.2
Western wheat grass	0.6	0.2
Purple lovegrass	...	0.2	0.1	0.1
Ticklegrass
Little barley	...	0.2	0.1	0.1
Brome grasses	...	1.5	1.4	1.0
Tumblegrass	...	0.4	0.2	0.2
Annual dropseeds	...	0.6	...	0.2
Bead grass	...	0.3	...	0.1
Six-weeks fescue	0.3	0.1
Total	(1.3)	(12.8)	(4.4)	(6.2)
Forbs	1.5	2.9	1.5	2.0
Grand Total	100	100	100	100.1

bluegrass, except at Denton, was in the Airport series where it was 67%. Thus, average amount of bluegrass (or blue grama at Denton) was 78%. The other 10% composition of increasers was shared by the other species in this group. Among these, side-oats grama had less than half its abundance in the good pastures. It had begun its period of degeneration.

One additional species of invading grass had appeared and, as will be shown, several weedy forbs. The part of the vegetation composed of invading grasses was now 6%. Forbs had not increased.

POOR RANGE CONDITION

The poor pasture is the last stage in the long story of degeneration of prairie. The best grasses have disappeared and even bluegrass has been weakened by excessive grazing and trampling. Even those of less

TABLE 5. Percentage composition of the vegetation in the poor pastures at Raymond, Airport, and Denton. The figures in each column are averages of 150 samples taken during the summer.

Species	Raymond	Airport	Denton	Ave.
DECREASERS				
Big bluestem	...	4.7	0.4	1.7
Little bluestem	...	0.4	0.1	0.2
Prairie dropseed
Tall dropseed
Needlegrass
Plains muhly
June grass	0.1	...
Indian grass
Total	(...)	(5.1)	(0.6)	(1.9)
INCREASERS				
Kentucky bluegrass	44.8	0.7	24.3	23.3
Side-oats grama	...	7.9	0.8	2.9
Blue grama	3.2	1.1	0.5	1.6
Scribner's & Wilcox'
Panic grass	0.3	3.0	0.1	1.1
Hairy grama
Sedges	...	6.0	...	2.0
Rushes	0.6	1.7	0.1	0.8
Total	(48.9)	(20.4)	(25.8)	(31.7)
INVADERS				
Sand dropseed	9.1	9.9	5.9	8.3
Western wheat grass	6.2	2.1
Purple lovegrass	0.5	0.9	0.5	0.6
Ticklegrass
Little barley	13.1	0.2	1.7	5.0
Brome grasses	8.7	...	4.1	4.3
Tumblegrass	0.5	1.1	7.5	3.0
Annual dropseeds	...	30.9	37.5	22.8
Bead grass	...	0.1	1.9	0.7
Six-weeks fescue
Crabgrass	0.3	0.1
Stinkgrass	...	0.1	0.6	0.2
Canada bluegrass	1.3	0.4
Total	(38.4)	(43.2)	(61.0)	(47.5)
Forbs	12.7	31.3	12.6	18.9
Grand Total	100	100	100	100

grazing value, the increasers, have been reduced in average abundance from 88% to 32. A host of low-grade invading grasses, mostly annuals, have replaced the highly nutritious ones and now constitute more than a third of the vegetation. With these are intermixed a large number (19%) of invading weedy forbs or non-palatable, weedy native forbs (Table 5). Bluegrass has suffered an average loss of one-half its former percentage of the total vegetation. Percentage of side-oats grama has been reduced to less than half its abundance in fair pastures.

Each pasture now has 6 to 10% of the quite palatable invader, sand dropseed. Little barley and species of *Bromus* (nearly all *B. commutatus* and *B. tectorum*) furnish some forage in spring and early summer. Actual yield of the far more abundant annual dropseeds is low despite their large percentage of basal area. These species in true prairie truly indicate poor pasture. The more or less continuous overstory of gumweed, ragweeds, ironweed, and many others is not only almost inedible but actually hinders the grazing animals in searching out the grasses. The percentages of these forbs per pasture range from 13 to 31. They must be very abundant to compose such a large basal area. To the ecologist and student of pasture management they alone at once indicate a poor pasture.

RÉSUMÉ

The decline of the two most abundant decreaseers, big bluestem and little bluestem, and the early gains and later losses of the two most abundant increasers, bluegrass and side-oats grama, are shown in Figure 11. The pronounced role of bluegrass in degenerating pastures is clearly evident.

A comprehensive view of the average abundance of increasers, decreaseers, and invaders and the consequent change in the composition of the vegetation, with its continued overuse, is shown in Figure 12.

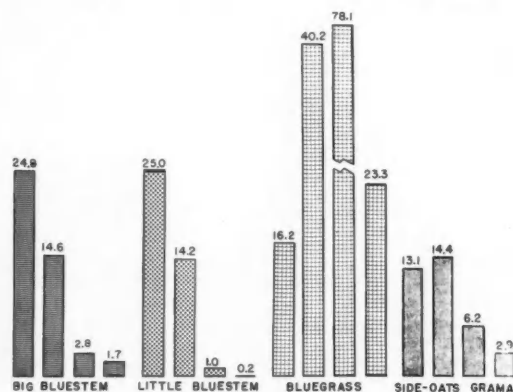


FIG. 11. Percentage composition of vegetation furnished by the two most abundant decreaseers (left) and the two most abundant increasers (right). Numbers at the top of the bars indicate the average percentage composition of the vegetation furnished by each species in excellent, good, fair, and poor pastures, respectively. Each bar represents the average percentage of three pastures.

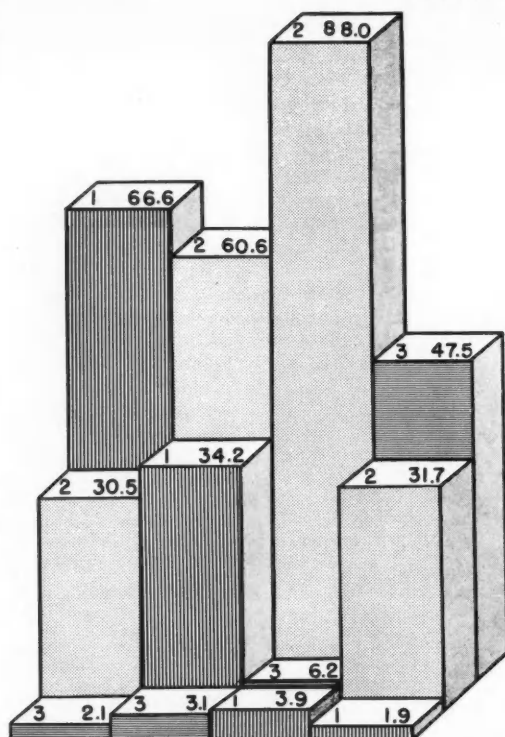


FIG. 12. Block diagrams showing percentage among grasses of decreaseers (1), increasers (2), and invaders (3), in excellent pasture (left), and in good, fair, and poor pastures, respectively. Each block represents the average of three pastures of one class. Numbers on the right side of the top of the blocks are percentages.

As the pastures degenerate, the best forage grasses, the decreaseers, are replaced by the second best ones, the increasers. Finally these give way, mostly to annual grasses and weeds.

OCCURRENCE OF FORBS

The portion of the basal area of vegetation composed of forbs was small in all range condition classes except poor. The average percentage for each class from excellent to poor was 0.9, 2.0, 2.0, and 18.9, respectively. When the percentages were based upon dry weight they were found, of course, to be very much greater. But since the total weight of forbs and not that of individual species was ascertained, their occurrence will be considerable here.

Among decreaseers only two important species were found to occur regularly. This is indicative of two things, first that the forb population had only partially recovered from drought, and second, that perhaps some species had declined greatly even in excellent pastures because of previous grazing. Thirteen legumes and 32 other forbs of common occurrence in true prairie are listed as decreaseers by Weaver & Hansen (1941). In fact, all but two or three of these occurred in a single, large, ungrazed

prairie near the Airport before the drought (Steiger 1930). Among a total of 18 species of common occurrence found in the present study, *Amorpha canescens* was most abundant. Its average occurrence was 22.6% in excellent pastures, but this decreased to 8.9 in good ones, and then to 0.9 and 0.4% in the lower classes. A second legume, but of less regular occurrence, was *Psoralea floribunda*. It was found in excellent and good pastures (7.1 and 1.3%) but little (0.7) or none occurred in fair or poor ones.

Increases were represented by 21 species. Of these only 9 occurred in 5% of the samples in at least one pasture. *Aster multiflorus* was found most frequently. It was present in 25% of the samples in excellent and good pastures, in 38 of the fair class, but it was of much less abundance or absent in the poor pastures. *Solidago glaberrima* was also widely distributed in excellent and good pastures and more widely in fair ones, but none was found in the poor class. *Achillea occidentalis* increased from about 3% to 24, but 10% was its occurrence in poor pastures. Occurrence of *Artemisia gnaphalodes* increased from 0.7% in the excellent pastures to 15 in the good ones. It then decreased to 6% in fair pastures and was absent in poor ones. *Hedeoma hispida*, *Xanthoxalis stricta*, and *Vernonia baldwini* increased rather consistently from excellent and good pastures where they occurred infrequently (0.7 to 3.3%) to fair ones (about 5 to 6%) and then increased in the poor pastures to 10.4, 6.9, and 16.4% occurrence, respectively.

Total species of invading forbs was 25, but only 12 occurred in 5% of the samples in at least one pasture. *Cirsium undulatum* and *C. flodmani*, *Ambrosia psilostachya*, *Euphorbia maculata*, *Leptilon canadense*, and *Verbena stricta* were the only ones in samples in excellent pastures. All except *Ambrosia* were infrequent; it was found in 30 to 57% of the samples in the lower range condition classes. No species of *Cirsium* was very abundant. *Ambrosia elatior* occurred in fair and poor pastures only, here its percentage occurrence was 5 and 25, respectively. *Euphorbia maculata* increased consistently from better pastures to the poorer ones. *E. marginata* and *Grindelia squarrosa* were found in fair and poor pastures only, but *Lepidium densiflorum* and *Plan-*

tago purshii occurred in one or two of the good pastures as well. *Verbena stricta*, one of the best indicators of degeneration of grassland, increased from 0.7 to 6, then to 10 and finally it occurred in 15% of the samples. For ease of comparison, part of the data on forbs is summarized in Table 6.

BASAL AREA, MULCH, AND BARE SOIL

The basal area of the vegetation was estimated at a height of 1.5 inches, rather than at the soil surface. This is the height usually employed, since it is about the level to which many plants are grazed, especially when the pasture is overstocked. This height more nearly represents the actual cross-sectional area of the base of many bunches, which may contract considerably just above the crown. Moreover, the area occupied by *Antennaria campestris*, *Euphorbia maculata*, and rosettes close to the soil are thus included in the basal area, which is the part of the soil surface occupied by living vegetation.

Basal area is one of the most permanent characters of most grasses in ungrazed climax prairie. For example, the number of stems in a bunch grass may vary from a few dozen to a few hundred in very dry and very wet years, respectively, and the yield may vary accordingly. But as long as the mature plant is alive, its basal area usually changes slowly if at all.

Increase or decrease in basal area in grazed grassland is a barometer of change. Its decrease may indicate either deterioration, as when openings appear in abused bluegrass, or regeneration when the same sod is being replaced by bunches of bluestems. Increase of basal area may denote deterioration in high-grade native pasture, as the replacement of bluestems by bluegrass or blue grama as shown in Table 7.

TABLE 7. Percent of basal area of vegetation in each of the four range condition classes in each series, and average basal area in each class.

Series	Excellent	Good	Fair	Poor
Raymond....	28.4	28.0	58.3	22.9
Airport.....	19.4	22.8	48.6	17.0
Denton.....	20.8	32.8	66.8	32.8
Average...	22.9	27.9	57.9	24.2

TABLE 6. Total number of species of each class of forbs in samples from each range condition class, and their average percent occurrence in the samples.

Class	RANGE CONDITION			
	Excellent	Good	Fair	Poor
Number of Species				
Decreasers...	11	12	4	4
Increases...	10	13	14	14
Invaders...	7	13	13	25
Average Percent Occurrence				
Decreasers...	30.6	10.8	2.3	1.1
Increases...	49.7	57.7	67.4	41.2
Invaders...	20.3	57.7	75.6	66.5

Data in Table 7 are the averages of the 150 samples in each pasture taken during the summer. Bluegrass was so widely spread in the excellent pasture at Raymond that the basal area was quite as great here as that in the good pasture. With this exception, basal area increased in each pasture from the excellent to the fair class. The increase was always greatest from the good to the fair class. This was usually followed by an even larger decrease from the fair to the poor class, with degeneration of bluegrass or short grass.

Typical predrought prairie always presented an almost continuous even if thin mulch despite annual mowing and removal of the crop of hay (Weaver & Fitzpatrick 1934). The mulch was examined and its

amount estimated in each sampling area after the plants had been clipped. Where there was a continuous cover of litter about 3 mm. thick, the mulch was considered as moderate. It was designated by the number 2. Where the undecayed or semidecayed debris was only about 1 mm. thick, there was always some bare soil. Here the amount of mulch was designated as little or 1. Where a sampling area had practically no mulch, the amount was designated as 0. Conversely, where the matted leaves, etc. formed a layer greater than 30 mm. and sometimes 5 cm. thick, the mulch was designated as excessive or 4. A heavy mulch (3) ranged from 4 to 30 mm. in thickness. The relative amount from each range condition class is shown in Figure 13. That from the excellent class of pasture, in the figure, is of coarse texture and was composed mostly of the leaves of prairie dropseed, tall dropseed, and big bluestem. That from the good class was of similar texture except that it contained also the finer leaves of bluegrass. That of lowest weight, from the fair range condition class was composed mostly of bluegrass and side-oats grama and had the finest texture of all. Mulch from poor ranges consisted largely of fragments of stems of coarse weeds but also included some finer material.

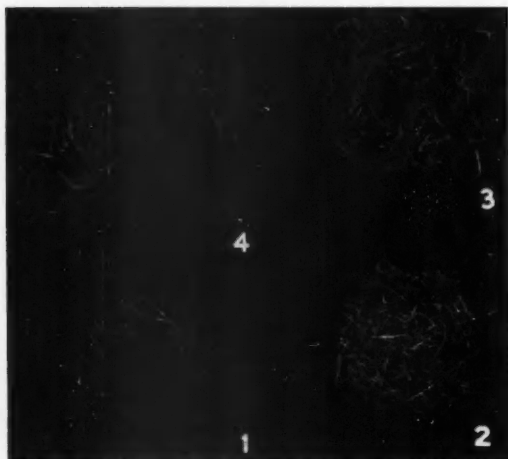


FIG. 13. Mulch from four range condition classes, each taken from 10, square-foot samples, showing relative amounts and texture. Weights from excellent to poor classes are 238, 89, 34 and 55 grams, respectively.

When the 30 numbers, representing the amount of mulch in the samples of a pasture, were added and the sum divided by 30, the average shown in Table 8 was obtained.

Mulch in the excellent pastures was often heavy and sometimes excessive, but never poor. The soil was well insulated from rapid and excessive changes in temperature; it was well protected from puddling caused by rain, and from erosion. A goodly amount of organic materials was furnished by the debris. The good pastures had usually a moderate mulch, but sometimes it was heavy in roughs. While the mulch decreased in each fair pasture of bluegrass or

TABLE 8. Average amount of mulch in each pasture, based on the 0 to 4 scale, and average for each range condition class.

Series	Excellent	Good	Fair	Poor
Raymond....	2.5	1.9	1.6	1.0
Airport.....	2.5	2.1	1.3	0.5
Denton.....	2.9	1.7	1.6	0.6
Average...	2.6	1.9	1.5	0.7

blue grama, the amount varied from moderate to little. In poor pastures it varied mostly from little to none. Average amounts of mulch from excellent to poor pastures were 2.6, 1.9, 1.5, and 0.7, respectively, on the 0 to 4 grading scale.

The percentage of bare or unmulched soil in each sample area was also noted and averaged for each pasture type. In excellent pastures only 0.9% bare ground occurred. In good pastures there was 3.3% and in fair ones 4.0. Even in poor bluegrass pasture, vegetation or some type of mulch covered all but 6.6% of the soil.

HEIGHT OF GRAZING

The height of the grass was recorded in each square-foot sample. If there had been no grazing, the ungrazed height was measured. If the vegetation had been rather uniformly grazed, the average height was obtained. Where part of the sample had been grazed and the rest ungrazed or one part grazed high and another low, the condition was noted and two measurements were made and averaged. Where the foliage of the grass was 3 inches or less in height, or this was the average where two heights maintained, the condition was recorded as low grazing. Where grazing averaged higher than 3 inches, it was recorded as high grazing. Height of the grass in any pasture varied, of course, at different times throughout the summer; here only averages will be considered. It should be made clear that grazing heights and amounts of unconsumed forage (which will be considered later) are related primarily to the degree of current utilization as well as past stocking intensity. Taken alone they are not valid indicators of range condition. They were ascertained for the purpose of showing their relation to range condition classes, during a good year for growth, as based on percentage composition of vegetation under usual grazing practices in eastern Nebraska.

It could reasonably be assumed that grazing would be closer as the amount of available forage became less. This was found not only for the average of classes of pasture but also (with two exceptions) for the individual pastures in each series. The average percent of samples grazed low was only 17 in the excellent class, but increased to 49 in good pastures and to 63 in the fair ones and finally to 76 in the poor ones (Table 9). The poor pasture at Raymond had more coarse weeds than either of the others; these prevented both general and close grazing to a considerable degree. The small number of

grazed samples in the excellent Denton pasture was due to understocking. The percentage of samples grazed closely in the fair Denton pasture is also low. Here blue grama rather than bluegrass prevailed. As previously described, this area was the portion of a large bluestem range where the heavily grazed bluestems had been replaced by the short grass. Since it is less palatable than the bluestems or bluegrass, grazing was not so general here.

TABLE 9. Percent of samples in each pasture in which grazing was low, and average percent in each series.

Series	Excellent	Good	Fair	Poor
Raymond.....	19.2	38.7	68.3	45.7
Airport.....	23.4	52.1	80.2	88.2
Denton.....	8.8	56.5	41.1	95.0
Ave. percent grazed low	17.1	49.1	63.2	76.3

The height of ungrazed grasses and average heights of grazing are shown in Table 10. Average height in inches of ungrazed grass decreased uniformly from excellent to poor pastures as follows: 9.9, 9.5, 5.9 to 4.5. A similar decrease in height of grasses grazed high is 5.9, 5.1, 4.6, and 4.6. The high grazing of grasses (4.6 inches), unexpected in poor pastures, occurred where coarse weeds, some of the previous year, prevented close grazing at least early in the season. Grasses grazed low were grazed closer with decrease in quality of pasture as follows: 2.9, 2.6, 2.5, and 2.2 inches, respectively. With minor exceptions, the same pattern occurs when the pastures in any series are considered individually (Table 10).

TABLE 10. Average height, in inches, of grasses in each pasture that were ungrazed, grazed high, and grazed low.

Series	Ungr.	High	Low	Ungr.	High	Low
	Excellent			Good		
Raymond.....	10.8	6.5	2.9	12.2	5.4	2.8
Airport.....	8.9	5.1	2.7	7.0	4.6	2.4
Denton.....	10.1	6.2	3.0	9.4	5.2	2.6
Average.....	9.9	5.9	2.9	9.5	5.1	2.6
Series	Ungr.	High	Low	Ungr.	High	Low
	Fair			Poor		
Raymond.....	7.8	4.6	2.6	6.3	5.0	2.1
Airport.....	5.2	4.8	2.0	3.6	3.9	2.2
Denton.....	4.8	4.5	2.8	3.7	5.0	2.2
Average.....	5.9	4.6	2.5	4.5	4.6	2.2

UNCONSUMED FORAGE FURNISHED BY GRASSES AND BY FORBS

It has been shown elsewhere that during spring and early summer, production of forage considerably exceeds the amount consumed. Only after midsummer does the current consumption of forage exceed

that presently produced. It is only then that the total amount of forage in the pasture begins to decline (Weaver & Darland 1948, Weaver & Bruner 1948). Unlike prairies mowed in autumn, in pastures the harvest begins in May and continues in some parts from day to day throughout the summer. In this study the yield was taken partly in June but also in July and August. Each time it was from different plots. It represents then, an average of the total amount of forage available for grazing at these times. It should be recalled that selective clippings were made in each sampling area and that each class of grasses and forbs was air-dried and weighed separately. The average percentages of unconsumed forage for the three months are shown in Table 11.

TABLE 11. Percentage of the total unconsumed forage furnished by each class of grasses and forbs in excellent to poor pasture, and the average in each range condition class. The series is indicated by the first letter of its name.

Class	Excellent Pastures				Good Pastures			
GRASSES	R	A	D	Ave.	R	A	D	Ave.
Decreasers.....	62.2	65.2	74.8	67.4	40.1	33.6	43.7	42.1
Increasers.....	21.8	23.1	12.1	19.0	31.2	33.1	34.9	33.1
Invaders.....	1.5	3.6	1.7	1.7	4.6	2.3	2.9	2.9
Total.....	84.0	89.8	90.5	88.1	82.0	71.3	80.9	78.1
FORBS								
Decreasers.....	11.2	8.6	1.5	7.1	0.6	3.6	3.6	2.6
Increasers.....	3.8	1.1	3.3	2.7	2.8	6.3	4.1	4.4
Invaders.....	1.0	0.5	4.7	2.1	14.6	18.8	11.4	14.9
Total.....	16.0	10.2	9.5	11.9	18.0	28.7	19.1	21.9
Grand Total....	100	100	100	100	100	100	100	100
Class	Fair Pastures				Poor Pastures			
GRASSES	R	A	D	Ave.	R	A	D	Ave.
Decreasers.....	3.0	3.4	4.0	3.5	1.9	0.6	0.8
Increasers.....	72.4	44.5	66.9	61.3	24.2	12.1	7.4	14.6
Invaders.....	1.2	11.2	5.1	5.8	20.5	14.9	20.1	18.5
Total.....	76.6	59.1	76.0	70.6	44.7	28.9	28.1	33.9
FORBS								
Decreasers.....	3.6	1.9	1.8	0.2	0.4	0.2
Increasers.....	17.2	6.2	7.2	10.2	2.1	5.6	12.1	6.6
Invaders.....	6.2	31.1	14.9	17.4	53.0	65.5	59.4	59.3
Total.....	23.4	40.9	24.0	29.4	55.3	71.1	71.9	66.1
Grand Total....	100	100	100	100	100	100	100	100

FORAGE FROM GRASSES

In excellent pastures, percentage of ungrazed forage furnished by the decreaseers ranged from 62 to 75 with an average of 67. In the good pastures these percentages ranged from 34 to 49 and the average was only 42. Forage of decreaseers was nearly all grazed in the fair pastures; only 3 to 4% remained. None was found in one poor pasture and the average amount was 0.8%.

Ungrazed forage of increaseers was least in the excellent Denton pasture (12%) and greatest at the Airport (23). The average was 19%. The average increased to 33% in the good pastures, where the

individual amounts were remarkably uniform. A higher average, 61%, was found in those of fair range condition. The percentage for the Airport pasture, where invaders were many, was lowest, 45. In poor pastures, even the forage of increasers (mostly bluegrass and side-oats grama) was much less. Percentages ranged from 7 to 24 with an average of 15.

Forage of invaders did not average even .1% in the excellent Raymond pasture. Average for all such pastures was 1.7. The average percent continued low (2.9) in the good pastures where none had more than 5. Even in the fair range condition, with one exception, the forage of invading grasses was low; highest yield was 11% and average 6. But in the poor pastures, yield of invaders was 15 to 21% with an average of 19.

In excellent pastures the several types of grasses furnished 88% of the total ungrazed forage (variation from 84 to 91%). It was somewhat less in the good class, 78% with a variation from 71 to 82 in individual pastures. Even in fair pastures the grass increment of ungrazed forage was 59 to 77% with an average of 71. But in poor pastures the average decreased to 34, the amount in the several pastures varying from 28 to 45%.

FORAGE FROM FORBS

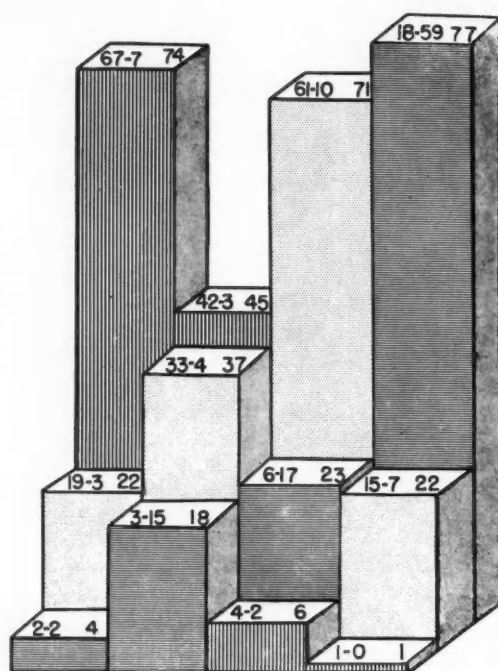
Ungrazed forage from forbs that decreased varied greatly in the three excellent pastures, being highest at Raymond (11%) and least at Denton (2). The average was 7%. There was less variation in the good pastures where the average decreased to only 3%. A further decrease to 2% occurred in the fair pastures and only 0.2% of the ungrazed forage in the poor ones was furnished by forb decreasers.

Conversely, the weights of forage from forb increasers, which averaged 2.7% in excellent pastures, became greater. The average weight was nearly doubled in good pastures where it was 4.4%. The percentage ranged from 6 to 17 in fair pastures but the average had increased to 10%. In poor pastures forage from increasers was less (2 to 12%) with an average of 6.6%.

Spectacular changes occurred in amount of ungrazed invading forbs. In excellent pastures the amount did not average more than 2% but in good ones the percentage was 15. It was scarcely higher (17) in those of fair range condition, but in poor pastures invading forbs composed 53 to 66% of the total weight of ungrazed vegetation.

RÉSUMÉ

A clearer conception of the relative amounts of unconsumed forage furnished by each of the three types of grasses and three types of forbs in the four classes of pasture (shown in Table 11) may be had by an examination of Figure 14. Here it may be seen that total decreasers composed (in round numbers) 74, 45, 6, and 1% of the uneaten forage in the excellent to poor pastures, respectively. Similar sequence of numbers for the grass increment is 67, 42, 4, and 1%. That for forbs is 7, 3, 2, and 0%.



EXCELLENT GOOD FAIR POOR

Fig. 14. Percentage of the total unconsumed forage from the sampling areas furnished by decreasers (vertical lines), increasers (lighter color), and invaders (horizontal lines) in each class of pasture. The numbers on the right side of the block show the total percent of decreasers, etc. in each series. The first number on the left shows the percentage of grasses, and the second the percentage of forbs comprising the total of each group.

Increasers furnished 22, 37, 71, and 22% of the total uneaten forage in each of the several classes of pasture, respectively. Grasses alone composed 19, 33, 61, and 15% of the total in the preceding sequence, and forbs 3, 4, 10, and 7%.

Unconsumed forage furnished by invaders increased rapidly, as the class of pasture became lower; percentages from excellent pastures to poor ones are 4, 18, 23, and 77. Similar sequence of percentages for the unconsumed invading grasses is 2, 3, 6, and 18, but for forbs they are much larger—2, 15, 17, and 59.

AMOUNT AND COMPOSITION OF UNCONSUMED FORAGE

Pastures remain in the excellent or good range condition classes only as long as they produce enough forage each year to provide an ample amount for current consumption without sufficient harm to the best-liked species to cause their serious deterioration. Hence, it is of interest to ascertain just how much forage remained uneaten, at various times during the grazing season, and its composition. The average

TABLE 12. Total amount (in grams) of grasses and forbs left unconsumed in the 150 samples from each class of pasture at the time of clipping in June, July, and August. Also average amount in each class and yield in tons per acre.

Class	June	July	August	Ave.	Tons per acre
Grasses					
Excellent...	2,169	2,926	2,961	2,685	.859
Good.....	1,251	1,704	1,445	1,467	.469
Fair.....	1,498	1,379	913	1,263	.404
Poor.....	754	768	704	742	.237
Forbs					
Excellent...	239	493	358	363	.116
Good.....	219	344	649	404	.129
Fair.....	228	670	708	535	.171
Poor.....	1,169	1,307	1,783	1,420	.454

amounts of grasses and forbs in each class of pasture are shown in Table 12.

In excellent pastures the amount of grass was more than a third greater in July than in June, but it scarcely increased during August. The most abundant grasses, bluestems and prairie dropseed, are warm-season species with vegetative growth continuing at least until mid-July, and even longer when grazed. From mid-June to late August an average of .86 ton per acre remained unconsumed. This amount, of course, included the bases of the plants. Many of the prairie grasses are not grazed closer than 2 to 3 inches and even bluegrass retains 1 to 1.5 inches of its basal portion in closely grazed pastures. The weight of this uneaten, living forage is equal to 10 to 20% or more of the total weight of the various mature grasses.

Unconsumed grass in good pastures was consistently smaller in amount than that in excellent ones. It was less than two-thirds the amount in excellent pastures at each of the three clippings. This is shown by the average, .47 ton per acre, which is only 55% as great as that in excellent pastures. A part of this decrease in good pastures may be attributed to a less vigorous growth of bluestems and other well-liked grasses, but especially to their replacement by bluegrass which yields only about 60% as much forage (Weaver & Hougren 1939, Weaver & Darland 1948). The slightly decreased amount of forage in August was probably due to a total smaller amount of forage available for consumption which resulted in closer grazing.

In fair pastures, where two-thirds or more of the grasses were the cool-season bluegrass, or blue grama, the bulk of the forage was produced much earlier than in good pastures. Hence, the amount uneaten by June was greater than that in good pastures. It also exceeded the amount in fair pastures in July. Here grazing was closer and high-yielding warm-season grasses were few. Average amount of unconsumed grasses (.40 ton per acre) was 53% less than in excellent pastures, and 14% less than in those of good grade.

In poor pastures the amount of ungrazed grasses in June fell to half that in the fair grade. This occurred despite the yield from a number of early growing annuals. In fact, it varied but little during the summer and averaged 41% less than in the fair grade pasture. It was only 28% as much (.24 ton per acre) as that in the excellent grade.

All classes of forbs composed (in round numbers) only 12% of the .98 ton total uneaten forage in excellent pastures, but 22% of the total amount (.60 ton) unconsumed in good pastures. This increase was due largely to perennial ragweed which is seldom grazed. These data are from Table 12 and are shown graphically in Figure 15. Forbs bulked higher in the .57 ton of unconsumed forage in fair pastures, where they furnished 30% of the total. In poor pastures the percentage of forbs was even higher. The coarse stems of ironweed, gunweed, and other weeds so greatly added to the weight of unconsumed forbs that it always far exceeded the amount in fair pastures.

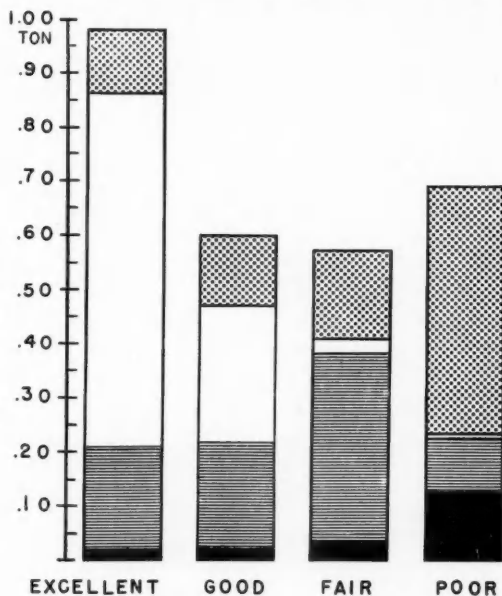


FIG. 15. Average amount and composition of ungrazed forage at the times of clipping. Invading grasses are shown in black and increasers by horizontal lines; decreasers are unshaded. All forbs are included in the checkered pattern. The scale is in hundredths of a ton per acre.

This unpalatable vegetation also increased greatly the total yield of .69 ton per acre, of which 66% was furnished by forbs.

Total annual yields in similar upland pastures where the vegetation was harvested once each month were approximately 1.5 tons per acre during good years. A similar amount of hay is often obtained from one cutting in late August or September.

While these data do not reveal the amount of forage left on the soil at the end of the grazing sea-

son, they do clearly indicate that the amount of uneaten forage would be greatest and the quality best in excellent pasture and least and poorest in poor ones. These conditions were clearly revealed in late fall. Many students of range management believe that the amount of forage left at the end of the grazing season is the best criterion by which to judge good or poor pasture management. Pastures become poor chiefly because of excessive removal of forage. Ordinarily about 25% should be left on the soil in true prairie (Weaver & Hansen 1941).

DISCUSSION

None of the 12 pastures selected for this study had previously been used for experimentation. Their grazing history is unknown, since records had not been kept. Degeneration from one class of pasture to the next lower one is ordinarily accomplished slowly over a period of years. The process itself under continued overuse of the grassland has characteristics which are probably almost universal.

The more palatable species are eaten down, thus rendering the uneaten ones more conspicuous. This quickly throws the advantage in competition to the side of the latter. Because of more water and light, their growth is greatly increased. They are enabled to store more food in their propagative organs as well as to produce more seed. The grazed species are correspondingly handicapped in all these respects by the increase of less palatable species and the grasses are further weakened by trampling as stock wanders about in search of food. Soon bare spots appear that are colonized by weeds or weedlike species. The weeds reproduce vigorously and sooner or later come to occupy most of the space between the fragments of the original vegetation. Before this condition is reached, usually the stock are forced to eat less palatable species, and these begin to yield to the competition of annuals. If grazing is sufficiently severe, these, too, may disappear unless they are woody, wholly unpalatable, or protected by spines (Weaver & Clements 1938, p. 470).

The degeneration of productive grassland has a profound effect upon the economy and welfare of the community. Once the early symptoms of deterioration are generally recognized, corrective measures may be taken to stop the downward trend and improve the range. The concept of four different grades of pasture or four distinctly different range condition classes has been extremely valuable to students of ecology, range examiners, and graziers as well. It presents a fixed concept of a pasture class or range condition with which another pasture may be compared. The placing of this concept on a percentage basis adds to its validity. It focuses attention more directly on each type of vegetation. Such a series of pastures is invaluable in teaching ecology and in an educational program on soil conservation. Cover of some sort is the chief tool used in conservation practice.

That one class of pasture degenerates gradually under poor management into the next lower one or may develop under protection or proper usage into

the one next higher, must be clearly comprehended. Thus, the good pastures in this study were not all equally good nor were the excellent pastures of the same degree of excellence. Only a little knowledge of classes of pasture plants and experience with composition of vegetation enables one to distinguish a good pasture from a poor one. But with each class further study reveals different degrees of deterioration or improvement. There is a considerable degree of variation in every range condition class. One soon recognizes high, intermediate, and low types of good pastures or of fair ones. If it is assumed that each pasture selected in this study was intermediate for its class (and this was the intent of the investigators), then the probable trends of decrease, increase, and invader may be plotted as shown in Figure 16. It may be seen that in the high type of excellent pasture the decreaseers composed about 80% of the vegetation and the increaseers about 20. There were practically no invaders. But in the low type of excellent pasture decreaseers had fallen to about 55% and increaseers composed about 40%. Thus,

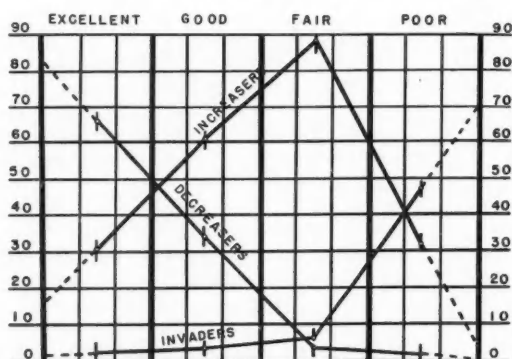


FIG. 16. Probable trends of grass decreaseers, increaseers, and invaders between actual points (average percentages) determined for the median of each class of pasture. Projections of these lines (which are broken) show the probable relation to the climax prairie on the extreme left and the low type of poor pasture on the right.

there are considerable differences among excellent pastures themselves. In the low type of poor pastures there are almost no decreaseers and only remnants of increaseers. Here the invading grasses alone compose about 65%. The native and invading forbs, (not shown in Figure 16) which composed only 1 to 2% of the basal area of the vegetation in other classes of pastures, now occupy 19% in the medium type of poor pasture (Table 5). Actually, it is probable that invading grasses and especially native and introduced forbs increase even more rapidly than the extended line graphs (broken lines) indicate. Earlier studies on composition of prairie (Weaver & Fitzpatrick 1934) showed that the grass decreaseers composed about 87% of the original prairie vegetation and increaseers and forbs the remainder. Since bluegrass has greatly increased since

1941 (after the drought) the 13% of increasers and forbs in prairie would seem quite probable.

The grasses and forbs of the northern mixed prairie that first decrease and may disappear under heavy grazing or drought have been listed by Allred (1945). He also lists grasses and sedges that increase following the first stage in depletion of excellent mixed prairie. The annual grasses and weed invaders that increase on these depleted grasslands are also listed. Dyksterhuis (1949), in his grouping of range plants, lists the most common decreasers and increasers among grasses in west central Texas, and some chief invading grasses and forbs. Changes in percentage composition of the vegetation according to certain species is given for excellent, good, fair, and poor range condition classes in the western Cross Timbers of Texas (Dyksterhuis 1948).

Forbs constitute an important part of the vegetation of true prairie. Nearly all legumes are valuable as forage and under predrought conditions they contributed a considerable amount of the total yield. In some prairies, which were clipped near the soil surface four times during the growing season, the lead plant alone supplied 200 pounds per acre of air-dry forage (Weaver & Albertson 1943). Forbs undoubtedly furnish a valuable variety to the diet of livestock. Costello (1942), working in Colorado, states: "Cattle grazing native grama and buffalo grass pastures in which weeds or shrubs are present have consistently shown better gains than those in pastures where the grass stands are nearly pure. Apparently, the relatively small amount of forage provided by the secondary species balances possible nutrient deficiencies that may occur when the diet is almost exclusively blue grama and buffalo grass." Runyon (1947) ascertained the chemical composition of *Aster multiflorus*, *Amorpha canescens*, and various other prairie forbs at Hays, Kansas. He states that the greatest contribution of the forbs to the diet of cattle seems to come from the higher percentages of calcium and phosphorus compared with that of blue grama.

Mulch or litter is a characteristic feature of grassland. Weaver & Flory (1934), in referring to mowed climax prairie near Lincoln, Nebraska, stated that "a mulch of fallen leaves, fragments of stems, flowers and fruits, etc., forms a more or less continuous cover of varying thickness. This may have a dry weight of 50 to 225 grams per square meter on uplands and over 1,000 grams on lowlands."

In native grassland pastures and ranges mulch or litter has proved to be one of the most reliable factors employed in determining the condition of the range (Humphrey 1949). An accumulation of mulch is abundant on excellent ranges and covers most of the soil surface not occupied by living plants. A good accumulation of mulch indicates that the past grazing use was not abnormally heavy. Amount of mulch or litter is now almost invariably considered as a criterion of range condition (Dyksterhuis & Schmutz 1947). It has been shown by Ellison (1944, 1945) that amount of infiltration and amount of run-

off on nearly all soils are determined by amount of raindrop erosion. Complete prevention of erosion is ordinarily possible only under a mulch sufficiently dense and close enough to the soil surface to prevent splashing of soil by raindrops. Over a wide difference in soil types, a mulch (according to Duley & Kelley 1939) had a greater influence on infiltration capacity than soil type, initial moisture content of soil, and rainfall intensity combined.

Butler (1948) ascertained the amount of residues (all dead materials including bunches, etc.) in spring in a very large pasture adjacent to one in the Raymond series. Here there occurred excellent, good to fair, and poor classes of range condition. Average amount of residues per square meter in each class was, in the preceding order, 980, 523, and 378 grams.

Little is known of the several stages in recovery of vegetation in true prairie that has been grazed for a long time. In fact only a few records of the degeneration of any particular true prairie area have been made (Weaver & Darland 1948). Recent studies on recovery of lowland prairie in the fair or bluegrass stage have been made by Mentzer (1950). Although nearly all of the bluestems had disappeared or were reduced to a condition of extremely low vigor, recovery was rapid. After two years of complete protection a good class of pasture had been re-established on this rich alluvial soil.

Recovery of protected upland pasture in the bluegrass stage (fair class) was studied by Weaver & Hansen (1941a) each year from 1934 to 1940. The work was continued by Weaver & Bruner (1945) from 1941 to 1943, and finally by Mentzer (1950) in 1948 and 1949. Despite the presence of a large area of contiguous climax prairie and the presence of many dominant grasses in the pasture subsere, the climax stage had not been attained even after eight years very favorable for growth.

The trend of the grassland subsere in the Fort Worth Prairie of northern Texas has been studied by Dyksterhuis (1946). He points out that little bluestem, the chief climax dominant, increases slowly from the low-grade or medium range lands to those in the late subsere, and then very rapidly until the climax is attained. In the development of the subsere he finds there is an increase in the percentage of grasses of greater stature, an increase in the proportion of perennials, and an increase in total plant cover. There is also greater forage production.

Allred (1948) in his excellent paper, "How to inventory grazing resources and develop a ranch conservation plan" states that determination of range condition is, in effect, a summary of the kind and amount of climax and other vegetation found on each site. The class of pasture is based entirely upon the percentage of climax vegetation; excellent pastures contain 100 to 75%, good pastures 75 to 50%, fair pastures 50 to 25%, and poor ones 25% or less.

In eastern Nebraska bluegrass pasture ranks only as good since production of forage even on lowland is only 65% as great as that in prairie (Weaver & Darland 1948). On upland the yield of bluegrass

relative to that of prairie is even less. Another reason for lower rank is that this mesic grass often dries and becomes dormant in midsummer. Moreover, recent experience shows that it dies during extreme drought, and leaves the soil almost bare.

SUMMARY

It has long been known that grazing of native grassland is a selective process and that the prairie is not grazed uniformly and evenly as the vegetation deteriorates in quality and is reduced in quantity.

Only recently (1941), however, have the grasses and forbs of the true prairie been divided, after years of study, into the very natural groups of grasses and forbs that decrease under overuse of the range (the decreaseers) and those that, benefiting from this release from severe competition, for a time become more abundant (the increaseers). If non-prairie species, which invade the grassland when the cover is opened by grazing, are included, a basis is laid for the classification of pastures into several range conditions.

Degenerating true prairie results in 4 types of pasture or range condition classes. The excellent pasture consists almost entirely of native prairie plants. A good pasture results when about half of the native species, mostly decreaseers, have waned and died and are replaced by bluegrass (*Poa pratensis*). Further overuse of the vegetation exterminates nearly all prairie species and the resulting fair pasture is nearly all bluegrass, but it has an increasing number of invading weedy grasses and forbs. Further degeneration results in a poor pasture with patches of bluegrass, weeds, and bare soil.

In the present research 12 pastures, 3 in each range condition class, were selected for study. The composition of the vegetation in each was ascertained and compared as regards species of grasses and forbs. The amount of vegetation available for forage during the growing season and the height at which it was grazed were ascertained, as well as the amount of litter or mulch left on the soil.

The grassland areas varied in size from 50 to 80 acres. Pastures representing 4 range condition classes of any one series were in the same immediate vicinity, but the 3 series were separated by a distance of 8 to 28 miles. All had originated from typical true prairie of eastern Nebraska, and were located near Lincoln.

The pastures occurred on moderately rolling upland with slopes of 2 to 10%. Each pasture was nearly square to broadly rectangular in shape. Distance to water was about three-fourths mile or less. The dominant soil type is Carrington loam or silty clay loam, a very productive soil which supports vegetation yielding from 1 to 1.5 tons of hay per acre.

Vegetation in each pasture is described. It was sampled in 150, square-foot areas which were uniformly and widely distributed at random along two lines, each of which crossed the pasture in a diagonal direction. One line in each pasture intersected the other on the top of a hill.

In each sample the species of grasses and forbs were recorded and the basal area occupied by vegetation was ascertained. Percentage composition of grasses and forbs was obtained by ascertaining the amount of total basal area (considered as 100%) furnished by each species. Average height of vegetation was measured. The plants were then cut selectively and bagged, air-dried, and weighed in 6 separate groups. These were grass decreaseers, forb decreaseers, grass increaseers, forb increaseers, invading grasses, and invading forbs. The percentage of bare ground, if any, was noted, and the soil mulch was estimated and recorded in 5 classes.

The chief decreaseers among the grasses in all pastures were big bluestem (*Andropogon furcatus*), little bluestem (*A. scoparius*), prairie dropseed (*Sporobolus heterolepis*) and tall dropseed (*S. asper*). Chief increaseers were Kentucky bluegrass and side-oats grama (*Bouteloua curtipendula*). Characteristic invading grasses of low-grade pastures were sand dropseed (*Sporobolus cryptandrus*), western wheat grass (*Agropyron smithii*), little barley (*Hordeum pusillum*), and species of Bromus.

The 3 individual pastures of each range condition in the 3 series were compared to obtained a definite idea regarding the composition of the vegetation in each and how little or how greatly it varied within its condition class. Decreaseers, increaseers, and invaders varied in number of species and their abundance in the several classes of pasture. Only species that furnished 5% of the vegetation in at least one sampling area were considered.

Among grasses there were only 8 decreaseers in any pasture and only 4 occurred abundantly. A total of 6 increaseers, aside from a few sedges and rushes, occurred. Only 3 were abundant. Of invading grasses 13 occurred, but only 6 in considerable abundance.

Average percentages of decreaseers in excellent to poor pastures were 24.8, 14.6, 2.8, and 1.7 for big bluestem. Little bluestem furnished, in the same order, 25.0, 14.2, 1.0, and 0.2% of the total vegetation. Percentages for prairie dropseed were 11.7, 2.0, 0, and 0.

Grass decreaseers as a group furnished 66.6% of the vegetation in excellent pastures, 34.2 in good ones, 3.9 in those of fair condition, but only 1.9 in the poor ones.

The tremendous increase of Kentucky bluegrass was from 16.2% in excellent pastures to 40.2 in good ones, and 78.1 in those of fair grade. It then decreased to 23.3% in poor pastures. Percentages for side-oats grama are, in the same order, 13.1, 14.4, 6.2, and 2.9. Since no other increaseer occurred in nearly such great abundance, it may be seen that bluegrass really dominated pastures of lower class than good.

Total increaseers averaged 30.5, 60.6, 88.0, and 31.7% in the several classes of pastures.

Invading grasses were few (2.1%) in excellent pastures and good ones as well (3.1); they increased to 6.2 in fair pastures and were extremely abundant

(47.5) in poor ones. Here annual species of *Sporobolus* alone averaged 22.8%.

Percentage composition of vegetation furnished by forbs averaged 0.9, 2.0, 2.0, and 18.9, respectively.

As pastures degenerate, the best forage grasses (the decreasers) are replaced by the second best (the increasers). Finally these give way, mostly to annual grasses and weeds.

Among a total of 18 species of forbs that decrease, *Amorpha canescens* was most abundant, with an average occurrence of 22.6% in samples in excellent pastures, but only 8.9, 0.9, and 0.4 in those of decreasingly lower range condition. *Psoralea floribunda*, the second most abundant, was much less plentiful. It decreased from 7.1 to 0 from excellent to poor pastures.

Increasers were represented by 21 species but only 9 were at all abundant. *Aster multiflorus* increased in occurrence from 25% to 38 and then became less abundant. *Vernonia baldwinii* increased from 0.9 to 1.5% in occurrence in excellent and good pastures to 4.9 and then 16.4% in fair and poor ones.

Of 25 species of invading forbs only 12 were ever abundant. Important among these were *Ambrosia psilostachya*, *A. elatior*, *Euphorbia maculata*, *Grindelia squarrosa*, and *Verbena stricta*. The 7 species in excellent pastures had an average occurrence of 20.3%; the 25 species in poor pastures, 66.5%.

Average total basal area in excellent pastures was 22.9%. It increased steadily with increase in bluegrass to 27.9 in good pastures and 57.9 in fair ones. In poor pastures basal area was 24.2 percent.

Mulch was classed as (0) none, (1) little, (2) moderate, (3) heavy, and (4) excessive. The average from all samples taken in excellent pastures was 2.6. In good pastures it was 1.9, in fair ones 1.5, and in poor ones 0.7.

Average percentage of samples where grazing was low (less than 3 inches in height) was, from excellent to poor pastures, 17.1, 49.1, 63.2, and 76.3, respectively. Average height of ungrazed grass decreased uniformly from 9.9 inches in excellent pastures to 4.5 in poor ones. Average height of low grazing decreased regularly from 2.9 inches in excellent pastures to 2.2 in poor ones.

Average percentage of total unconsumed forage furnished by grass decreasers was, from excellent to poor pastures, 67.4, 42.1, 3.5, and 0.8. That from increasers was 19.0, 33.1, 61.3, and 14.6. Invaders at first yielded little (1.7%); this amount increased to 2.9, 5.8, and finally to 18.5%.

Total amount of ungrazed forage in excellent pastures furnished by all grasses was 88.1%. This decreased to 78.1 in good pastures and to 70.6 in fair ones. In poor pastures it was only 33.9% of the total, but varied from 28 to 45 in individual poor pastures.

Unconsumed forage from forbs that decrease was 7.1, 2.6, 1.8, and 0.2% in the several classes of pastures. Increasers composed 2.7, 4.4, 10.2, and 6.6% of the total unconsumed forage. Invading forbs at

first bulked low, 2.1 and 14.9%. In fair pastures the percentage was 17.4 and in poor ones 59.3.

Total amount of unconsumed forage furnished by the several classes of forbs was 11.9, 21.9, 29.4, and 66.1%.

These data for each pasture in each series, like data on percentage composition, were shown clearly by an arrangement of block diagrams.

The average amount of grasses left unconsumed at the time of clipping in June, July, and August was ascertained. In excellent and good pastures where warm season grasses were abundant it was highest in July and August. In fair pastures, where bluegrass dominated, it was highest in June and decreased greatly in August. In poor pastures amount of unconsumed grasses was uniformly low. Total amounts in excellent to poor pastures were, in tons per acre, .86, .47, .40, and .24, but in poor pastures .45 ton of various forbs also occurred.

The ecology of every species of grass, including its behavior under different degrees of grazing, is fascinating as pure science. Application of this knowledge is of great practical value.

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THE LIFE HISTORY AND ECOLOGY OF THE JUMPING MOUSE, *ZAPUS HUDSONIUS*

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INTRODUCTION

Jumping mice of the genus *Zapus* are widely distributed over northern North America, occurring as far north as the Arctic Circle (Anthony 1928), and as far south as Raleigh, N. C.; Wheeling, W. Va.; Jackson Co., Mo.; Santa Fe, N. Mex.; Kern River, Calif. (Preble 1899) and Athens, Ga. (Petrides 1948). In certain areas they may be among the most numerous of small mammals (Hamilton 1935). According to Preble (1899), the first reference to North American jumping mice seemingly was made by Thomas Pennant, in the latter part of the 18th century, who mentioned the animal under the name of the "Long-legged Mouse of Hudson's Bay." Since then, numerous articles concerning various aspects of the animal's life history and ecology have been published. In-

cluded are the works of Preble (1899), Sheldon (1934), Hamilton (1935), Sheldon (1938), Blair (1940a), and others. Despite these, many phases of its life history and ecology remained relatively unknown.

The writer recognized the opportunity and need for a comprehensive study in 1941 when the investigation was initiated. Certain parts of Minnesota provided excellent habitats and afforded opportunities for field observations. Except for the period June 1942 to July 1946, the animals were studied at various times from 1941 to the latter part of the summer of 1948; the most intense and comprehensive investigations occurring in the spring, summer, and fall of 1947. Where practical, an attempt is made to present the data quantitatively. The natural history

sections are largely descriptive. The data presented were secured by the repeated live-trapping and examinations of marked individuals in the field, observations of caged animals, and examining dead specimens. The methods used are described under the various sections. In the study 124 marked individuals were trapped and examined a total of 393 times, 40 live-trapped individuals and 17 young born in captivity were caged for periods of one day to over a year, and 179 (including 9 casualties among the marked animals) dead specimens were examined.

For help during the study, the writer wishes to especially thank the following: Dr. W. H. Marshall for much helpful advice and timely criticisms; Drs. A. C. Hodson and L. L. Smith for many suggestions; Dr. Gustav A. Swanson for advice during the initial phases of the study; Dr. C. O. Rosendahl for the identification of many plants; Harvey L. Gunderson for preparing the majority of the photographs; the Cardinal brothers, Marcel, Andrew, and Buddy for permitting me to work on their farm; my wife, Mary Jane, who aided with the live-trapping, care of captives, keeping of records, and preparation of figures. The cooperation of several others is acknowledged in the text.

DESCRIPTION OF SPECIES

The jumping mouse, *Zapus hudsonius*, is a small mouse-like rodent with greatly enlarged hind feet and an exceptionally long tail (see measurements) (Fig. 1). The forelegs are relatively short. The ears are somewhat conspicuous. The body is clothed in moderately long, somewhat dense hair of a rather coarse texture and several colors. The dorsal portions are marked by a broad stripe of brownish hairs many of which are tipped with black giving this region a grayish-black appearance. The sides are bright yellowish-orange, whereas the underparts and feet are white. The tail is bicolor, dark above and light below, and sparsely covered with hair which is longer on the terminal part. The vibrissae are prominent. The mammae are 8, and quite prominent in lactating females (Fig. 2). The anterior or pectoral pair are just behind the front legs and the most posterior pair are inguinal. The male genitalia are inconspicuous except during the breeding season when the scrotal sac becomes enlarged (Fig. 2). The testes en-



FIG. 1. Captive Jumping Mouse (Photo by H. L. Gunderson).



FIG. 2. Breeding Jumping Mice Showing Enlarged Mammae of Females and Enlarged Scrotum of Male. Male on Right. (Photo by H. L. Gunderson.)

large and may be either abdominal, inguinal, or scrotal during this period. The upper incisors are deeply grooved anteriorly and of a yellowish-orange color. The premolars are wanting except for Pm^4 which is small and peg-like; the dental formula being

$$I \frac{1}{1}, C \frac{0}{0}, Pm \frac{1}{0}, M \frac{3}{3}, x 2 = 18$$

The body weights are variable, not only for different animals, but for the same individual from time to time depending upon the season or its activity. During the latter part of summer both sexes become excessively fat (see hibernation) whereas they may be quite thin in the spring following the long period of winter inactivity. Breeding females increase in weight late in gestation (see reproduction). These facts make it difficult to set up standards of average weights. It seemed desirable to include animals collected throughout the season to obtain "mean" adult weight. Only those "obviously" mature, weighed under laboratory conditions soon after being caught, and for which accurate measurements were available are used. Females in advanced pregnancy were excluded. Since all weights were of mice trapped in the field it follows that those "fat enough" to hibernate were likewise excluded. The mean weights of 32 males and 34 females collected near St. Paul and Centerville, Minnesota in 1947 and 1948 were 16 (11.5 to 19.2) and 18.9 (12.5 to 24.8) grams respectively.

The body dimensions vary considerably among "mature" jumping mice, more so than would normally be expected for individual differences. It is suspected that their growth continues for some time after the first season. This belief is strengthened by the work of Dice (1936) which shows that the deer mouse, *Peromyscus maniculatus gracilis*, grows after the second year of life. Many specimens were not suitable for measurements because a portion of the tail was missing. This seemed most common among the males and there is some evidence that it results from fighting (see sociability). Hamilton (1934)

reports the same condition for woodchucks and cites Howell as having observed the same for the meadow mouse. The mean measurements of the 66 adults for which weights are given were approximately the same for both sexes: total length; males 214.9 mm., females 219.2 mm., tail; males 127.5 mm., females 128.2 mm., hind foot; males 30.1 mm., females 30.1 mm., ear; males 13.1 mm., females 12.8 mm.

Examination of 334 trapped in the field, of which 325 were sexed with reasonable certainty, indicated a sex ratio slightly in favor of the females (110 to 100); 170 were females and 155 were males.

LIFE HISTORY

GESTATION PERIOD

To determine the gestation period, females were trapped and placed in small cages in the laboratory until they gave birth or it was evident they were not pregnant. Those not pregnant, and those that destroyed their young, were transferred to a larger cage containing males, usually for one night. Females that gave birth and did not destroy the young were not placed with males since it was desired that they raise the young with little disturbance. Six litters were born but information on two is too scanty for significance so far as gestation is concerned. The others supply pertinent information (Table 1).

TABLE 1. Period of gestation for four litters of jumping mice born in captivity.

Litter Number	Date Female With Males	Date Litter Was Born	Gestation Period (Days)
1	Night of June 21 and 22	July 9 12:00 A.M. ?	Between 17 and 18
2	Night of July 7 and 8	Between 5:00 P.M. July 25 and 1:35 P.M. July 26	Between 17 and 19
3	Trapped and Caged July 12	Between 3:25 P.M. July 31 and 6:00 A.M. August 1	At least 20 to 21
4	June 6 to June 14	June 26 ?	Not less than 12 or more than 20

Litter No. 1. A female, that had given birth to and destroyed a litter between June 14 and 16, was placed with males on June 21 at 12:00 A.M. for 24 hours. On July 3 she appeared to be pregnant. On July 9 at 2:00 P.M. she was observed with young estimated at no more than 2 hours old. The period between the time when placed with males until observed with young was 18 days and 2 hours, the upper limit for gestation. The period between the time when removed from the cage with males until observed with young was 17 days and 2 hours, the lower limit for gestation. Both of these extremes are improbable since jumping mice are mostly nocturnal. Copulation was probably during the night making the most likely period of gestation 17 days 12 hours ± 6 hours; i.e., if the young were 2 hours old when found.

Litter No. 2. This female gave birth to a litter about June 26 but did not raise the young. She was placed with several males about 5:00 P.M. July 7 for 24 hours. Between 5:00 P.M. July 25 and 1:35 P.M. July 26 she gave birth to young, indicating a gestation period between 17 days and 18 days 20.5 hours. Since the conditions were the same as discussed above, it can again be assumed that either of these extremes is unlikely. The time of birth is known only within 20.5 hours. An average figure for the most likely gestation period is 18 days 3.25 hours ± 6 hours.

Litter No. 3. A female was trapped and caged July 12. Between 3:25 P.M. July 31 and 6:00 A.M. August 1 she gave birth. The gestation period was at least 20 or 21 days. This female was lactating when caught and the longer gestation period could result from this condition. Svihla (1936) has shown that gestation is prolonged by lactation in the white-footed mouse, *Peromyscus maniculatus oreas*; perhaps the same is true for the jumping mouse.

Litter No. 4. A female trapped in the summer of 1946 was placed with various males between April 25 and June 6, 1947. Frequent inspections during this period revealed no signs of sexual activity. On June 6 her external genitalia appeared enlarged. This was thought to indicate the beginning of an oestrous cycle and she was placed with two recently trapped males until June 14. June 28 she had young estimated to be about 48 hours old because of their size and general appearance (one weighed 1.1 grams). This would indicate a gestation period of not less than 12 or more than 20 days. It is suspected that it was closer to the maximum figure since the female appeared to be in breeding condition when placed with the males.

The data for Litters 1 and 2 indicate the gestation period for non-lactating jumping mice of the genus *Zapus* is approximately 18 days. Litter No. 4 is also suggestive of such a figure. Litter No. 3 suggests that gestation is prolonged in lactating females. Data presented by Sheldon (1938a) indicate that the closely related *Napaeozapus* has a gestation period of 23 days or less.

DESCRIPTION OF YOUNG

Five litters born in captivity supply information on the young. Two, comprising 7 individuals, were eaten or deserted soon after birth. Of the remaining litters, totaling 10 individuals, 7 were raised beyond the weaning stage. One was born dead, another was taken for a specimen at the age of 1 day, and the third similarly at 23 days. In the successful litters only one newborn mouse was taken from the nest for examination. Following the initial examination, they remained undisturbed for about 1 week. Then examinations of the entire litter every 2 or 3 days were tolerated if the female were isolated. At each examination the following were recorded: standard measurements, weight, condition of skin, hair, eyes, ears, claws, incisors, voice, and general activity. Since the observations and measurements were made mostly on living specimens, they are not necessarily pre-

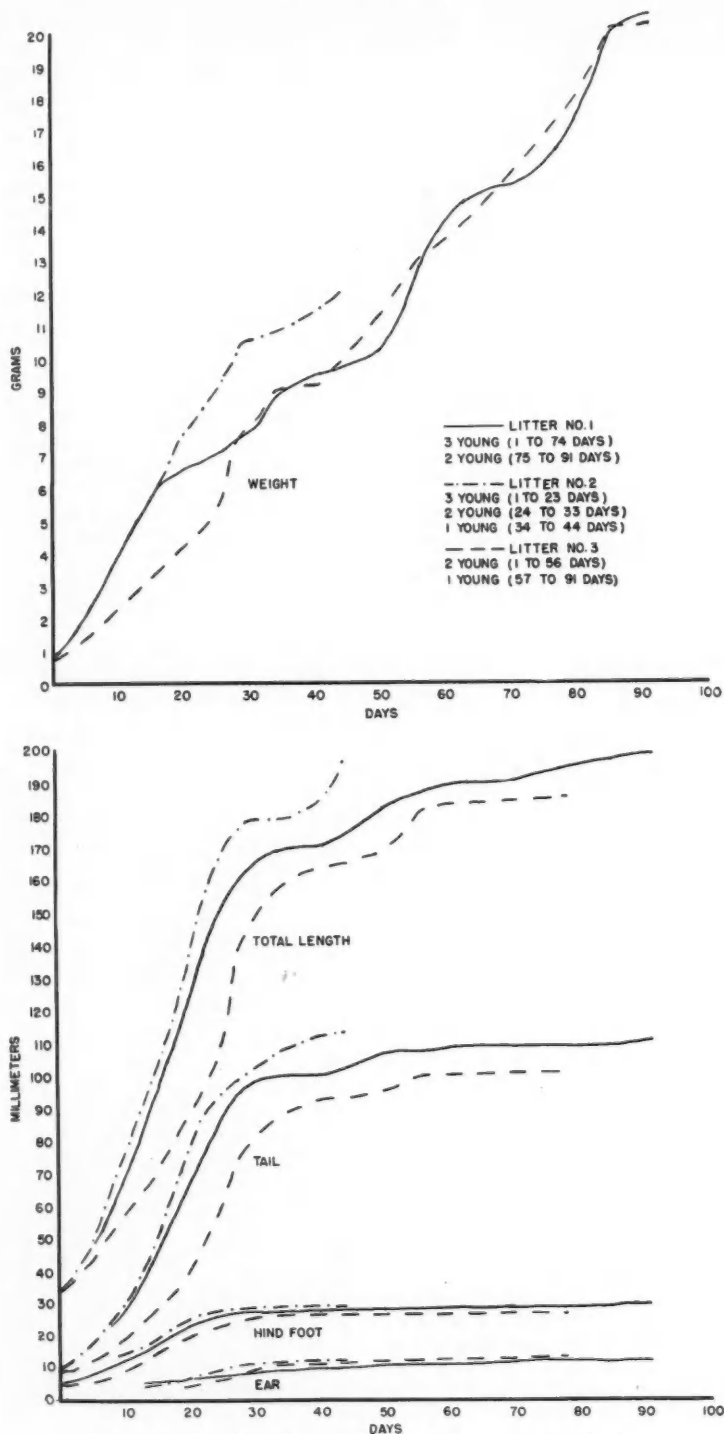


FIG. 3. Growth rates of young jumping mice.

cise, particularly the measurements. The growth rates and rate of maturity of the 3 litters were slightly different (Fig. 3). The following descriptions are based on average figures of the available material.

NEWBORN YOUNG

At birth, the young are completely hairless except for the minute vibrissae which can be clearly seen only with a hand lens. Svihla & Svihla (1933) in describing the young of *Zapus trinotatus trinotatus* state that the vibrissae of newborn young of that species are not visible. Likewise Hamilton (1935) describes the newborn young of the closely related *Napaeozapus* as having no vibrissae. Petrides (1948) states that day-old young of *Zapus hudsonius americanus* are entirely naked. The body is pink. The eyes are closed, appearing as darkened spots. The external auditory meatus is closed and the pinna of the ear is folded. The toes are fleshy, without claws, and the tail is short in relation to body length as compared to an adult. The average tail length was 59% of total length for 3 adults but only 27% for 3 newborn young. The young are helpless. A high-pitched squeaking sound, audible for several feet, can be heard (Fig. 4).

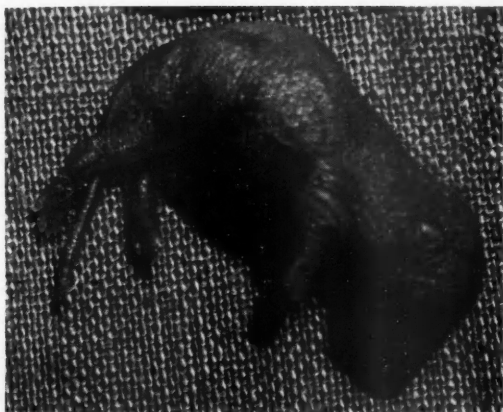


Fig. 4. Newborn Jumping Mouse. Scale mm. (Photo by H. L. Gunderson.)

The average measurements of 3, from different litters, are: total length; 34 mm. (34, 34, 34), tail; 9.2 mm. (10, 8.5, 9), hind foot; 4.7 mm. (4.5, 4.5, 5). Petrides (1948) gives the following measurements for one newborn young of the subspecies *Zapus hudsonius americanus*; total length 34 mm., tail 10 mm., hind foot 5 mm.

The average weight of 6 from 3 litters was .78 grams (.65, .8, .8, .8, .8, .9). Sheldon (1933) gives weights of 7 newborn of the same species as .7 grams each. Svihla & Svihla (1933) give weights of .7, .8, .8, .8, .9 grams for newborn young of *Zapus trinotatus*.

DEVELOPMENT DURING FIRST WEEK

The vibrissae grow until they are visible to the naked eye. The color of the body changes to flesh

and the dorsal parts become heavily pigmented, giving these regions a dark gray color. The tail becomes bicolor, the upper half being dark. The pinna of the ear unfolds and is tipped with black. The claws make their appearance. The young are able to crawl but unable to support themselves on their legs. In addition to the squeaking sound, a "suckling note" is made (Fig. 5).



Fig. 5. Seven Day Old Jumping Mice. Scale mm. (Photo by H. L. Gunderson.)

DEVELOPMENT DURING SECOND WEEK

Tawny yellow hair appears about the 9th day on the dorsal parts. By the 13th day it has spread to include the sides. Very sparse hair of a lighter color appears on the belly, back of feet, and outer surfaces of the legs. The vibrissae are prominent: measuring 5 mm. on the 9th day and 8 mm. on the 13th (measurements of one). The eyes remain closed but a crack down the center is visible by the 13th day. The claws have grown considerably, the longest on one measuring 1.5 mm. The incisors erupt about the 13th day, the lowers coming in slightly before the uppers. They are white. The activity has increased considerably but the young animals are still unable to support themselves on their legs. They continue to make a "suckling note" and squeak when pinched or handled (Fig. 6).



Fig. 6. Fifteen Day Old Jumping Mice. Scale mm. (Photo by H. L. Gunderson.)

DEVELOPMENT DURING THIRD WEEK

The hair covering is completed about the 17th day when the inner surfaces of the legs are haired. The darker hairs of the dorsal stripe begin to appear between the 15th and 19th days. The vibrissae continue their rapid growth; the longest on one measuring 11 mm. on the 19th day. The external auditory meatus begins to open about the 19th day. The young were observed to react to sound on the 20th. The longest claws measure about 1.5 mm. on the 19th day and the incisors about 1.0 mm. At this age the young are able to support themselves on their legs and make "hops" of about one inch as well as walk. The movements are quite awkward being accentuated by the size of the hind feet, which appear enormous for such small animals. The ratio length of hind foot to total length is 19% at 3 weeks while only 13% at birth. Prior to this time the young are not readily identified but the completion of the juvenile pelage, the rapid development of the hind feet, tail, and ears as well as the increased activity mark them as young jumping mice (Fig. 7).

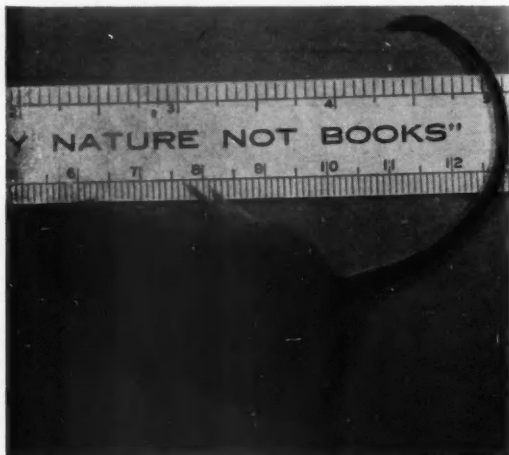


FIG. 7. Twenty-two Day Old Jumping Mouse. (Photo by A. L. Buzicky.)

DEVELOPMENT DURING FOURTH WEEK

The juvenile pelage is replaced by the adult pelage between the 23rd and 27th days. The eyes open between the 22nd and 25th days. In one litter of 3 the eyes were one-half open on the 22nd day and completely open on the 23rd. Two of another litter had their eyes completely open on the 22nd day while the eyes of the remaining mouse in the litter did not completely open until the 23rd. The eyes of a third litter, comprising two, did not open until the 25th day. With the opening of the eyes the entire aspect of the young changes for they venture from the nest for the first time and are seen to eat solid foods. At this age the incisors change from white to the yellowish-orange adult color suggesting that the

color change is correlated with the change in food habits. Pm^4 , M^1 , M^2 , M^1 , and M^2 were well developed and through the maxillary and dentary bones while M^3 and M^4 were developing but not through the bone in the skull of a 23 day old mouse. All teeth were well developed and through the bone in the skull of a 33 day old mouse.

The nursing period did not necessarily end as soon as the young were able to consume solid food. The young of one litter continued to suckle for the seven days they were allowed to remain with the female after they were seen to eat solid food. This gradual change in diet was also observed in the other two captive litters. These observations are substantiated by field data. On three occasions young estimated at 23 days old were live trapped (Nos. 56, 63, and 66 Centerville Study Area), while a nest containing 5 young estimated at 25 days old was found on the Centerville Area (see home sites). This latter group was undoubtedly able to leave and forage for themselves but had not as yet broken the family tie. Whether the female was still with this group is unknown. She was not seen but it is possible that she escaped when the nest was found.

By the close of the 4th week the young, except for size, have all the appearances of an adult and are capable of an independent existence.

RATE OF GROWTH

The greatest increases in body dimensions occurred during the first four weeks from both the standpoint of increment and percent (Fig. 3). The slowing down of the growth process occurred simultaneously with weaning.

An examination of the data (Fig. 3) at birth, at the end of 4 weeks, and at the end of 13 weeks reveals the following: At the end of the 4th week the mean length had increased approximately 4.6 times since birth while at the end of the 13th week it was only 5.8 times the length at birth. Approximately 75% of the increase in total length occurred in the first 4 weeks. The length of the tail increased approximately 10 times during the first 4 weeks and only 12 times in the 13 week period. Eighty percent of the increase in the tail length occurred in the first 4 weeks. The hind foot increased 5.6 times in length during the first 4 weeks and only 5.9 times in 13 weeks. Ninety-three percent of total increase in hind foot for the 13 week period occurred in the first 4 weeks. The ear increased proportionately more (29%) than any other dimension after the first 4 weeks. Since no ear measurements were taken until the 2nd week, the amount of increase during the first 4 weeks is unknown.

The greatest percent increase in weight occurred during the first 4 weeks and a noticeable drop occurred at the end of the 4th week in increment of increase. Beginning with the 7th week, weight increase again became rapid (Fig. 3). Just how much of this latter weight increase was due to growth is problematical. Certainly not all of it since jumping mice store quantities of fat in preparation for hibernation (discussed in another section). The retarding

of weight increase during the 5th and 6th weeks was possibly due to physiological adjustments brought about by the change in diet.

NUMBER OF YOUNG PER LITTER

Three sources supplied data on the number of young per litter; nests with young found in the field, litters born in captivity, and embryo counts of dead females.

The data from 3 litters found in nests in the field are at hand. One containing 6 young was found by the late Russel M. Berthel and George Rysgaard 6 miles east of Emmons, Freeborn Co., Minn., August 9, 1941. Another with 5 young was found by Mr. Karl W. Kahmann near Hayward, Wis., July 28, 1941. The 3rd was found near Centerville, Minn., August 16, 1947 by Buddy Cardinal. It contained 5 young.

Five litters, for which information on litter size was obtained, were born to caged females during 1947 as follows: June 21, 4; June 26, 3; July 9, 4; July 26, 2; and Aug. 1, 4.

Embryo counts for 14 pregnant females are available as summarized.

Date Collected	Number of Embryos	Greatest Length
June 5, 1947	7	1 mm.
June 5, 1947	5	4 mm.
June 10, 1947	7	3 mm.
June 16, 1947	6	10 mm.
July 23, 1947	5	6 mm.
Aug. 8, 1947	5	7 mm.
Aug. 9, 1947	4	2 mm.
Aug. 15, 1947	7	15 mm.
Aug. 15, 1947	4	15 mm.
June 2, 1948	5	7 mm.
June 2, 1948	7	2 mm.
June 2, 1948	6	10 mm.
June 3, 1948	7	3 mm.
June 4, 1948	6	4 mm.

The data from litters found in the field and from embryo counts compare favorably. Their means are 5.3 and 5.8 young per litter respectively. These data are not entirely comparable, however, since the number of embryos does not necessarily represent the number of young that will be born due to the possibility of resorption. Miller (1946) working with the pocket gopher, *Thomomys bottae navus*, gives evidence which indicates that a certain percent of embryos are resorbed by pregnant females of that species. Data are not sufficient for conclusions so far as the jumping mouse is concerned but the possibility cannot be overlooked.

The data from young born in captivity indicate a smaller mean litter, 3.4, suggesting that captivity influences litter size. This is further suggested by the fact that the 2 smallest litters (2, 3) were borne by a female in captivity since the preceding summer. No one of the other 3 had been in captivity for more than a month when the litters were born and conception had taken place previous to the time of capture for 2 of these. The size of the litter, 4 in each case, for these 3 was smaller than all but 1 for the other 2 types of data.

From these small samples, it seems that the data from litters born in captivity are not reliable for conclusions regarding litter size. The data of litters born under natural conditions and embryo counts in-

dicate that the average litter size is 5 or 6. This figure compares favorably with previously published data. Brimley (1923) records 1 lot of 7 embryos and 1 lot of 8 young for *Z. hudsonius americanus* in North Carolina. Bailey (1929) reports 6 embryos for a female *Z. hudsonius campestris* in Minnesota. Svihla & Svihla (1933) report a litter of 6 young for *Z. trinitatus* in Washington. Ivor (1934) found a nest containing 5 young in Ontario. Borell & Ellis (1934) give embryo counts of 6, 6, 4, 4, and 7 for *Z. princeps nevadensis* in Nevada. Sheldon (1934) gives embryo counts of 1 and 6 for *Z. hudsonius* in Nova Scotia. Townsend (1935) reports an average of 4.4 embryos per pregnant *Z. hudsonius* examined in New York. Hamilton (1935) records embryo counts of 4, 2, 4 and 4 and litters of 2 and 5 for *Z. hudsonius* in New York. Sheldon (1938) reports 2 litters of 7 young each for *Z. hudsonius* in Vermont. York (1945) records a litter of 6 young for *Z. hudsonius* in Canada. Petrides (1948) reports a litter of 6 young for *Z. hudsonius americanus* in Georgia.

NUMBER OF LITTERS PER YEAR

Only data obtained by the repeated examination of live-trapped females were considered suitable for conclusions on the number of litters produced by an individual during the breeding season. The likelihood of reaching erroneous conclusions regarding the breeding habits of a species from the examination of dead specimens has been pointed out by Burt (1940).

An investigation of the reproductive behavior of individual females was carried on simultaneously with home range and population studies at Centerville in 1947 (described in another section). Fifty-one live-trapped females were examined at various times during the course of the study. The number of such examinations per individual ranged from 1 to 15 with a mean of 4. The number of days covered by the individual examinations ranged from 1 to 113 with a mean of 19. In some cases the data are too scanty because of too few examinations or because the examinations did not extend over sufficient periods. In no instance was it possible to follow the activities of a female for the entire breeding season.

Each time a female was caught all information relative to her breeding condition was recorded. This included weight, whether embryos were palpable, and condition of mammary glands. From these data it was possible in most instances to summarize her breeding status. In others it was not readily determined since no single character satisfactorily expressed a definite condition.

In general, females in advanced pregnancy, were excessively heavy (Table 2). No. 41, for example, weighed 29 grams on June 23 and the next day, following parturition, weighed 20.7 grams. This was not the case in all instances as there were exceptions. The best example is provided by a caged female whose weight was .2 grams less 2 days before parturition than at the beginning of gestation. She

gave birth to an abnormally small litter of 2. It was also found that fluctuations of 1 or 2 grams in weight from day to day were not unusual. These were probably correlated with the amount of material in the alimentary canal and were of no reproductive significance. Jumping mice become excessively fat in the latter part of the summer (see hibernation), in preparation for hibernation. It follows that weight alone was not sufficient to determine pregnancy.

TABLE 2. Representative examples showing data for determining the breeding condition of adult female jumping mice live-trapped and examined during the summer of 1947, Centerville, Minn.

No.	Date	Mammary Glands Enlarged	Weight (grams)	Embryos Palpable	Week Young Were Born	Breeding Status
17	June 5	—	16.3	—	—	No external indication of sexual activity
	June 6	—	16.4	—	—	"
	June 7	—	14.7	—	—	"
	June 8	—	—	—	—	"
	June 12	—	17.7	—	—	"
	June 18	+	22.2	+	—	Pregnant
	June 19	+	22.1	+	—	"
	June 20	+	17.5	—	June 15-21	Suckling young
	June 23	+	—	—	—	"
	June 23	+	29.0	+	—	Pregnant
41	June 24	+	20.7	—	June 22-28	Suckling young
	June 25	+	19.9	—	—	"
	June 26	+	21.3	—	—	"
	June 29	+	18.2	—	—	"
	July 9	+	21.0	—	—	"
	July 10	+	22.2	+	—	Pregnant
	July 14	+	23.5	+	—	"
	July 15	+	26.0	+	—	"
	July 16	+	24.5	+	—	"
	July 17	+	21.2	—	July 13-19	Suckling young
	July 18	+	19.6	—	—	"
	July 19	+	18.2	—	—	"
	July 22	+	18.0	—	—	"
	July 23	+	18.0	—	—	"

The presence of embryos could usually be detected in advanced pregnancy by feeling the abdomen but in some instances produced doubtful conclusions.

The condition of the mammae was readily amenable to quantitative measurements. When not enlarged, a non-breeding condition was assumed. Enlarged mammae indicated reproductive activity and could often be interpreted to indicate the particular phase. Enlarged and lactating mammae indicated the female was suckling young or was in advanced pregnancy. Enlarged and non-lactating mammae indicated that the female had suckled young or was pregnant.

Inasmuch as no one of the above conditions were sufficient to establish the precise breeding status of an individual, a combination of all, in addition to her previous history, were utilized. The record of No. 17 (Table 2) will serve as an example. She was examined on June 5, 6, 7, 8 and 12. On these dates her mammae were not enlarged, weight not excessive (16.3, 16.4, 14.7, —, 17.7 grams), and no embryos were felt. These data are sufficient to conclude, so

far as external evidence is concerned, that she was in a non-breeding condition. On June 18 her mammae were enlarged but not lactating, her weight excessive (22.2 grams), and embryos could be felt obviously indicating that she was pregnant. A day later all conditions were approximately the same but on June 20 she was lactating, had lost considerable weight (weight=17.5 grams), and no embryos could be felt. The history and data indicated that she had given birth and was suckling young.

Data are sufficient to indicate the sexual activity of 30 females for June. For some of these additional data are available for July and August as discussed in subsequent paragraphs. Four of this group had young during the week June 15 to 21, 15 had young during the week June 22 to 28, 2 gave birth during the week June 29 to July 5, and 9 produced no young during the month.

Only 1 of the 4 that had young during the week June 15 to 21 was handled sufficiently during July to determine her breeding status and she produced a 2nd litter during the week July 20 to 26. No information is available for any of this group after July.

Five of those that produced young during the week June 22 to 28 were handled frequently enough during July to justify conclusions regarding their reproductive activities. Three each had a 2nd litter during the week July 13 to 19. One produced a 2nd litter during the week July 20 to 26 and the remaining one had a 2nd litter during the week July 27 to Aug. 2. No further data are available for this group.

One of the 2 that had a litter during the week June 29 to July 5 gave birth to a second litter during the week Aug. 3 to 9. No further data are available for the other one.

Additional information is at hand for 4 of those that produced no young in June. Two each gave birth to a litter during the week July 20 to 26. Two each produced a litter in July (data not sufficient to designate approximate date) and one of these produced a 2nd litter during the week Aug. 17 to 23. Nothing is known of the other 3 in this group for Aug. or later dates.

Sufficient information was obtained for 8 females during July for which no data are available for June. Three produced litters during the week July 13 to 19. Their activity for later dates is unknown. One produced litters during the weeks July 13 to 19 and Aug. 17 to 23. Another was judged to be a juvenile on July 23 but produced a litter during the week Aug. 17 to 23. The 6th gave birth to a litter sometime during July (data not sufficient to designate approximate date) and a 2nd during the week Aug. 3 to 9. The 7th produced a litter in July (data not sufficient to designate approximate date) and a 2nd during the week Aug. 10 to 16. The last had a litter during July 20 to 26 but nothing is known about her for Aug.

Data were secured for 6 females during Aug. for which no previous information were available. Two of these were adults and had litters during the weeks

Aug. 17 to 23 and Aug. 10 to 16 respectively. The remaining 4 were young of the year and each gave birth to a litter during the week Aug. 10 to 16.

A summary of the above information reveals that 7 females known to have had litters in June were examined sufficiently in July to determine their breeding status. Without exception they produced a second litter in July. No one of this group was examined in Aug. but it is quite possible that some or all had a third litter during this month. It is assumed that no females produced young in September since considerable evidence is available to support this contention (discussed in a later section). Four females known to have not given birth to young in June were examined in July and all produced young during the month. The only one of these for which data are available for Aug. had a second litter during this month. Two litters seems to be the maximum number that could be produced during the season by this late breeding group. All 7 adults examined for the first time in July gave birth during the month. Three of these were examined in Aug. and all had a second litter. It is possible that some or all of this group could have had an early litter making 3. Two adults handled for the first time in Aug. each had a litter during the month. Five young of the year from early litters were handled sufficiently to justify the conclusion that all had young during Aug.

The data indicate that most adult females (70% of those examined) breed soon after emergence from hibernation and produce the first litters within a month. The remaining females do not breed immediately but produce the first litter during the second month after emergence. This group might constitute young of the late litters of the previous breeding season but no data are available to support this assumption. Both early and late breeding females produce at least 2 litters per year. Those that breed early may quite possibly have 3 litters. This is suggested by the fact that the interval between the first and second litters did not exceed a maximum of 42 days for 9 of the 11 females known to have 2 litters and in most instances it was much less. For the other 2, data are less exacting, but 40 days seems to be about the upper limit between the 2 litters. Further data to support the evidence that jumping mice breed soon after parturition are available from caged animals. One gave birth to 2 litters within 26 days and another had 2 within 31 days (see gestation period.) The possibility of 3 litters per year is further intimated by the fact that there were 3 peaks of births during the breeding season (discussed in a following section).

AGE AT FIRST PARTURITION

There is some evidence from the Centerville live-trapping data to indicate that young of early litters breed during their first summer. The best example is afforded by No. 66 caught first on July 23. This mouse was obviously just out of the nest, since she was still in juvenile pelage; her age was estimated at about 23 days on the basis of pelage and size.

When next seen, on Aug. 15, her mammae were enlarged, weight greater (12.5 grams) than the average for mice of 46 days (10.5 grams), and it was believed that embryos were felt. These data seem sufficient for concluding that she was pregnant. Unfortunately she was not caught again. Nos. 74, 75, 76, and 78 were each caught one time on Aug. 9, 9, 10, and 12, respectively; all were judged to be young of the year because of their small size. No. 75, weight 18.5 grams, was in an advanced stage of pregnancy; embryos could be felt and her mammary glands were enlarged. Nos. 74, 76, and 78, weights 15, 15, 16.5 grams respectively, were thought to be in early pregnancy because of enlarged mammary glands and swollen abdominal regions but no embryos were felt.

Other data indicating that some young breed during the first summer are available from snap-trapped specimens. Three pregnant females were judged young of the year. One (wt.; 16.5 grams, measurements; 213-131-29-12 mm.) caught Aug. 8 contained 5 embryos (7 mm.). Another (weight; 15 grams) taken Aug. 9 contained 4 embryos (2 mm.). A third (wt. 16.5 grams) caught Aug. 20 had recently given birth to young as indicated by the enlarged and highly vascularized uterus (uterine horn 3 mm., body of uterus 4 mm. in diameter) and enlarged and lactating mammae.

These data indicate that some young produce litters at the age of approximately 2 months. All available information indicates that only young of the first litters breed during the first summer since no evidence has been found that any jumping mice are born in this latitude in Sept. (see extent of breeding season).

EXTENT OF THE BREEDING SEASON

Three sources supplied data for delimiting the breeding season; investigation of the reproductive activities of live-trapped females, an evaluation of the age of young caught on the trapping plots at various times, and examination of the reproductive organs of dead females snap-trapped throughout the summer. Only data secured at Centerville in 1947 are included because it is probable that each breeding season is slightly different due to the fact that the date of emergence from hibernation varies from year to year. In all cases the data have been reduced to a common denominator; i.e., it is expressed in terms of the approximate date of parturition. It is believed that the data are sufficient to indicate the peaks as well as the extent of the breeding season by recording the approximate dates of birth of the 119 litters and/or individuals that were or would have been born as determined by observations extending throughout the summer.

The procedure for determining dates of birth by examining live-trapped females has been described. The approximate date of birth (within 1 week) was determined for 46 litters by this method as follows: 4; June 15 to 21, 15; June 22 to 28, 2; June 29 to July 5, 7; July 13 to 19, 5; July 20 to 26, 1; July 27 to Aug. 2, 2; Aug. 3 to 9, 6; Aug. 10 to 16, and 4; Aug. 17 to 23.

Twenty-two of 62 snap-trapped females caught from May 29 to Sept. 28 supplied positive breeding data. Examinations of the uterine horns and mammae indicated whether they were pregnant and/or suckling young. In pregnant females the embryos were measured (greatest length) and designated as early (1 to 5 mm.), advanced (6 to 10 mm.), or late (11 to 15 mm.). For non-pregnant females the appearance and diameter of the uterine horns as determined by gross examination were recorded. These data were used in conjunction with the condition of the mammary glands for determining whether parturition recently had taken place. If the mammary glands were enlarged and lactating, uterine horns more or less anemic and 1.5 mm. in diameter or less it was concluded that parturition had taken place 1 to 3 weeks previously. If the female were suckling young and the appearance of the uterine horns was highly vascular and 2 mm. or more in diameter it was concluded that parturition had taken place within a week. If the mammary glands indicated that a female had but was not suckling young it was assumed that the young had been weaned within a week. These data were used in predicting the approximate date of birth (within 1 week) for the 22 litters as follows: 5; June 15 to 21, 6; June 22 to 28, 1; Aug. 3 to 9, 7; Aug. 17 to 23, and 3; Aug. 24 to 30.

The date of birth was estimated for 51 young of the year caught from July 14 to Sept. 28 by comparing their weights with a standard prepared from the weights of known age young raised in captivity (Fig. 3). For this group the estimates were made within 2-week periods because the data as a whole were not amenable to a finer grouping. The number of litters represented by this group is unknown. It is probable that some were included in the litters computed from the examination of live-trapped females but this seems of minor importance so far as defining the breeding season and indicating the peaks of reproduction are concerned. The approximate dates of birth are as follows: 12; June 1 to 14, 11; June 15 to 28, 5; June 29 to July 12, 16; July 13 to 26, 6; July 27 to Aug. 9, and 1; Aug. 10 to 23.

The data from estimating the age of young indicate that the earliest litters were born in early June (1 to 14). The data from the 2 other sources do not support this contention but indicate that the first young were born on or after June 15 suggesting the ages of some of the young were overestimated. The data from the repeated handling of live-trapped females should be more accurate on the average than that of the 2 other methods. The writer feels that it should be followed more closely especially since it is supported by the evidence from dead specimens. The trapping record indicated that the first females emerged from hibernation about May 25 which further discredits the possibility that many young were born during early June.

No litters were known to be born after the week Aug. 24 to 30. The data from dead specimens indicate that 3 were born during this week. Fifteen dead

adult females and 13 subadults were examined during Sept. and no one of these gave any evidence to indicate that young were born during this month. The evidence from hibernation indicates that in this latitude time does not permit the rearing of a litter so late in the season for neither the parent nor the young would have sufficient time to make physiological adjustments necessary for this condition (see hibernation).

The information available suggests that the dates June 15 to Aug. 30 approximately define the period during which parturition occurred. The data indicate that young were born throughout the period but not at a uniform rate. By plotting the number of litters and/or individuals for each 2 week period delimited by these dates it is seen (Fig. 8) that there are 3 peaks of births; one in the latter part of June, a second in mid and late July, and a third in mid Aug. Although the data suggest that the greatest peak occurs in June followed by lesser peaks in July and August, this is not necessarily true but could possibly be due to insufficient information for the latter periods. Evidence presented in a preceding section suggests that the heights of the peaks might be reversed in an undisturbed population. This seems logical because only 70% of the over-wintering females were found to produce litters during the first month after emergence from hibernation (only these litters contribute to the first peak). The remaining females produce the first litter during the second month after emergence and many or all that produced an early litter have a second litter during this period (both contribute to the second peak). Some or all of the late breeding females have a second litter in August. Some of the young of the year from early litters have young during this month. It is suspected that some of the early breeding females have a third litter at this time. If this assumption is correct there are 3 classes of females contributing young to the third peak.

These data apply specifically to the region of Centerville, Minn. during the summer of 1947 and probably do not apply in other latitudes and during other seasons. This assumption seems logical due to the hibernating habits of the animal. The breeding season must of necessity coincide with that period during which the animal is not in or preparing for hibernation. This could possibly account for some of the differences of opinion relative to the extent of the breeding season and the breeding habits of individuals. Preble (1899) states, "The birth of the young . . . usually takes place in May or June. Sometimes, however, it occurs as late as September; from which it seems probable that a second litter is raised, or that the breeding season continues throughout the summer." Brimley (1923) records 1 lot of 7 embryos for Sept. 17, 1891, and 1 lot of 8 young taken with an adult female June 13, 1895 for the subspecies *Z. hudsonius americanus* in N. C. Bailey (1926) reports as follows in regard to *Z. hudsonius campestris* in N. Dak., "The five or six young are brought forth . . . usually in May or June, and are barely full grown by the time their winter sleep is

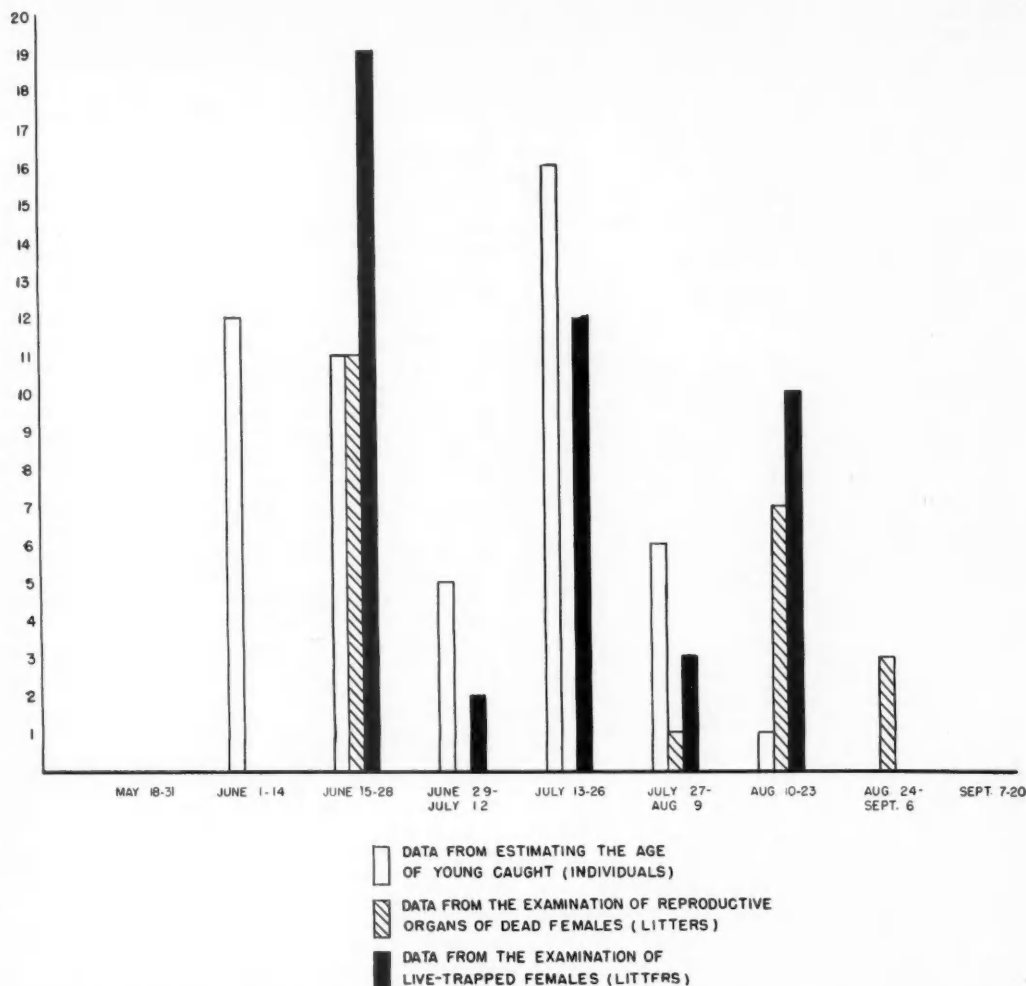


FIG. 8. Number of litters and/or individual jumping mice that were or would have been born during each two week period during the summer 1947 as determined by 119 observations.

to begin. In this latitude it is doubtful whether more than one litter of young is raised in a summer." Borell & Ellis (1934) studied *Z. princeps nevadensis* in Nev. They report, "Between June 22 and 27, five half grown young were captured. Between June 3 and July 4, five pregnant females were taken. . . ." Townsend (1935) reports that pregnancies were observed throughout the summer months in N. Y. for *Z. hudsonius*. Hamilton (1935) gives data for *Z. hudsonius* in N. Y. He reports 4 females with embryos, 2 with placental scars, and 2 litters observed in nests. He concluded that the young are born in early June and that but 1 litter is raised annually in N. Y. Sheldon (1938) gives the following information for *Z. hudsonius* in Vt. A nest of jumping mice was dug up Sept. 16, 1926 which contained 7 blind young. Sept 19, 1928 4 jumping mice, 2 of

which were no more than $\frac{2}{3}$ grown, were found in a nest. An immature jumping mouse was brought in by a cat Oct. 13, 1932. A *Zapus* caught July 15, 1936 gave birth to 7 young the following night. Blair (1940a) studied the breeding habits of *Z. hudsonius* in Mich. He concluded, "Both the sexual condition of the females and the number of immature and young adult animals indicate a peak of breeding activity in the spring and another in late summer, with an intervening period of very little sexual activity in midsummer." Petrides (1948) records 6 young born to a female *Z. hudsonius americanus* about Sept. 29, 1944. This female was captured Sept. 22, 1944 near Athens, Ga.

The evidence presented by some of the above workers indicates that the breeding season for certain localities includes later dates than that shown

for Minnesota in the present study. Earlier breeding dates are suggested. The work of Blair indicates a discontinuous breeding season with peaks in "the spring and late summer."

LONGEVITY

During April, June, July, and Aug. 1948 Plot 2 Centerville was snap-trapped (2,450 trap nights) to determine whether any of the jumping mice marked during the summer of 1947 (see home range) were resident on the plot. Only 2, Nos. 53 and 58, were caught. No. 53 was marked July 12, 1947. At this time she was an adult breeding female indicating she was at least in her second summer. She was therefore 2 or more years old Aug. 13, 1948 when snap-trapped. No. 58 was likewise an adult breeding female when marked, July 14, 1947, and was also 2 or more years old when snap-trapped June 2, 1948.

These 2 examples supply definite evidence that these mice may live for at least 2 years under natural conditions. On the other hand, the fact that only 2 were caught in 1948 plus the data discussed under stability of population and population structure indicates that only a small proportion of the population reach this age.

ECOLOGY

LOCOMOTION

The saltatorial powers of jumping mice are well developed and have been frequently described. All agree that they are capable of making extended leaps but there is a diversity of opinion as to the distance covered by a single bound. Preble (1899) states that *Zapus* when disturbed will jump 6 or 8 feet and under some circumstances perhaps much farther. Seton (1909) says that the jumping mouse creeps through the grass like a deer mouse or bounds away 10 to 12 feet at a bound. Bailey (1926) states that no roads or runways are used but they go through the grass with long leaps, or little hops, and occasionally with a slow creeping motion on all fours. Townsend (1935) observed jumps of about 2 feet on the part of one.

Many observations do not substantiate the longer jumps. The writer has never seen one jump farther than about 3 feet. On several occasions fully mature mice were released and pursued on level ground to ascertain their jumping ability. Many observations were made under more or less natural conditions. The greatest jumps were made initially when suddenly startled while in a squatting position. This first jump normally covered a distance of 2 to 3 feet and occasionally exceeded 3 feet by a few inches. Subsequent leaps were shorter but more rapid. A jumping mouse in full retreat always progressed by rapid jumps of about 1 foot. Under ordinary circumstances when not frightened, the usual means of progression was by little hops of 1 to 6 inches. They were frequently observed to crawl through or under the grass and other vegetation flattening their bodies close to the ground and proceeding on all fours.

SWIMMING ABILITY

On several occasions jumping mice were observed to take to the water when released from traps or when frightened from retreats. These observations and other evidence, discussed under habitat preference, indicate that they are somewhat aquatic.

To more accurately observe the methods of swimming, 5 were transported by boat out into a lake and released, one at a time. By rowing the boat along side it was possible to closely observe them. In all instances the animals proved to be excellent swimmers both on and underneath the surface. The methods of progression were similar to land movements; i.e., the limbs were employed differently at various times depending upon the speed. When first placed in water they moved rapidly by lunges produced by sweeping strokes of the hind limbs employed simultaneously. This movement was accomplished similarly to the long jumps made on land. Hamilton (1935) reports that the hind limbs are of primary importance in swimming and the fore feet are not employed. Following the first excited lunges, they settled down to a steadier and slower gait using all 4 limbs one at a time. The anterior part of the body was held high in the water. Preble (1944) observed a swimming jumping mouse and reported that both the fore and hind feet were employed in the swimming movement. The long tail trailed limply behind contributing in no way to the animal's movements. When approached too closely, they attempted to escape by diving. The maximum distance noted was about 4 feet. The depth was not determined. While underneath the surface they had a silvery appearance due to air bubbles clinging to the pelage (previously reported by Preble (1944)). One was able to swim vigorously for approximately 3 minutes after which it tired greatly and was in danger of drowning. Hamilton (1935) states that these mice can remain in the water for 4 or 5 minutes, perhaps longer.

DIGGING ABILITY

The fact that these rodents frequently inhabit underground burrows is discussed under home sites. Frequent observations of caged animals revealed the technique of construction. The mouse selected a spot, frequently a depression, and began to excavate the soil by means of the front feet, throwing it out behind. This process continued until the hole was deep enough to enclose the anterior half of the mouse at which time the hind feet were also brought into action to throw the loose dirt out of the burrow.

DEFENSE MECHANISMS

Jumping mice are seemingly docile creatures but there is some evidence that they will defend themselves when attacked. A subadult became imprisoned in a live-trap with an adult meadow mouse, *Microtus pennsylvanicus*. Ordinarily when this happened no intolerance was shown but on this occasion interspecific friction developed and in the ensuing struggle the jumping mouse was killed and badly mutilated about the head. The much larger meadow mouse, although not mortally wounded, suffered a severe gash

in the upper lip, evidently inflicted by the incisors of the jumping mouse. Even so there is little reason to suspect that these small rodents could successfully defend themselves against a predator by offering physical resistance. Their best defense seems invested in their ability to evade an enemy by rapid jumps (see locomotion), taking advantage of escape cover, and maximum use of their protective coloration.

When closely pursued they retreat by jumps of a foot or so rapid enough to require a man to run to keep abreast. This speed doubtless outstrips some potential predators.

In almost all instances when released from traps, they immediately retreated into the nearest available cover and soon disappeared. If they were familiar enough with the terrain to deliberately proceed to suitable holes or other protected spots, as Burt (1940) described for the wood mouse, *Peromyscus leucopus*, it escaped the attention of the writer. Only on 3 occasions does the writer recall having seen one deliberately and unhesitatingly proceed to a hole or any other retreat when released from a trap. In all other cases it seemed they instinctively retired into the most likely available cover without forethought or premeditation.

Another habit of a defensive nature, doubtless of great importance, was that of flattening themselves against the ground and remaining motionless, often for several minutes. In this position the white belly was completely concealed and the dark back and lighter sides normally blended into the surroundings in such a way that they were difficult to observe. This protective adaptation was usually observed when the mice were released in areas with sparse cover. The mouse normally made 2 or 3 bounds, crouched, and remained still if not pursued. This habit was previously reported by Sheldon (1934).

ACTIVITY PATTERNS

Jumping mice were occasionally frightened from their hiding places during the day and on a few occasions were seen abroad but all records including trapping, field observations and observations of captives indicate they are mostly nocturnal. Almost all daylight activity of captives occurred on cloudy, damp days. Ordinarily they remained in their quarters during the day seldom venturing out until after dark, but on cloudy days they frequently came out to feed and move about. The same was probably true under natural conditions but too few data are available for comparison and conclusions. The nocturnal activity likewise seemed to be greater on cloudy, damp nights for almost invariably greater numbers were caught in traps during wet periods.

VOICE

These animals seem more or less silent except when young (see development of young). During the years they were frequently handled, only one adult was heard to utter a sound. A female made a "clucking" sound on several occasions while kept in the laboratory. It was always made when the mouse was excited and seemed to come from the back

part of the throat. The mouse had a slightly deformed nose from having been caught in a trap, suggesting that the sound was unnatural but Sheldon (1934) described a similar sound made by captives. Svihla & Svihla (1933) report that captives made a squeaking noise when fighting. Sheldon (1934) also says that these mice squeak and further states, "When about to go into hibernation they squeak continuously if the nest is uncovered."

SOCIABILITY

Evidence from live-trapping with multiple-catch traps indicates that jumping mice are more or less solitary for only on 1 occasion were 2 caught in a single trap during 1 night (2 adult females). By contrast, 431 single catches were made.

There is very little evidence, on the other hand, to indicate that they are antagonistic towards each other. During the 3 summers that caged animals were under observation only 1 case of intraspecific strife was noted. For the most part, they lived in harmony regardless of sex, age class, or number in the cage. In most instances all residents occupied the same retreat and new additions were accepted, seemingly without reluctance. The one exception developed when 2 recently trapped adult males were placed in the same cage during May soon after the emergence date. One was definitely hostile towards the other. When approached too closely, he would rush at the other and bite or attempt to bite him on the rump. It is suspected that he "bit off" about 1 inch from the other's tail since this portion became detached and no other explanation seemed plausible. This single demonstration of intraspecific hostility occurred at the outset of the breeding season. Perhaps they exhibit territoriality during this period.

METHOD OF FEEDING

These rodents characteristically seize the material to be eaten with the front feet and devour it while reclining on their haunches (see Fig. 1). The following observation of a caged animal is typical of their feeding habits. The mouse selected a head of yellow foxtail, *Setaria glauca*, from several in the cage, separated it by gnawing through the supporting stem, seized it with the front feet, held it up to the mouth and began to gnaw at one end, stripping all parts from the rachis. The grass head was slowly rotated and shifted sideways until nothing remained but the rachis which was discarded. Actually the seeds were the only parts eaten and many of them fell to the ground as they were detached by the gnawing activity, along with the discarded accessory parts. No attempt was made to retrieve the fallen seeds. Instead, the mouse selected another head and continued its feeding activities.

WATER CONSUMPTION

Caged jumping mice regularly drank water from small containers. In all cases observed the process of drinking seemed similar to that of a cat or dog in that they appeared to lap the water. Whether they lapped or sucked the water was not readily determined. Usually they perched on the side of the

vessel and drank continuously until their thirst was satisfied.

MOLT

During the summer of 1947 all live-trapped, snap-trapped, and caged animals were examined macroscopically for molting. To a certain degree, a constant replacement of hair was in progress during early summer, followed by a heavy complete molt in late summer previous to hibernation. Preble (1899) stated that the fall pelage is usually assumed before entering winter quarters.

During May, June, July, and the first part of Aug. almost all animals examined showed some degree of molt; i.e., some hair was being lost and replaced by new hair of a brighter and more lustrous color. This was particularly noticeable on the sides. This gradual replacement of hair during these periods did not seem to be a general molt. It seemed to be of a replacement nature to take care of worn and lost hair. Borell & Ellis (1934) reported that 5 specimens taken between June 21 and July 12 in Nevada were molting. The old hair was thin, worn, and in some specimens spotted. The new hair could be seen coming in beneath the old hair, and it was growing uniformly over head, back, and sides.

Late Aug. and early Sept. were marked by a heavy molt of a general nature in which all hair was lost and replaced. The date varied with individuals but on the average it began about about Aug. 15 and was generally completed in about 3 weeks for those on which data were complete. No well developed molt lines, such as those common to pocket gophers, were observed, but the head and other anterior parts were the first to be covered with new hair followed by the middle portions and finally the rear areas. Following this molt, the mice had a more sleek and well groomed appearance. The colors of the pelage were brighter and the contrasting areas such as the white belly and dark dorsal portions stood out more clearly.

CLEANLINESS

Caged jumping mice appeared to be quite "particular" about their "personal appearance." They did not allow themselves to become dirty and unkempt. On several occasions, various individuals were observed to wash themselves by wetting the front feet and passing them over their faces and bodies. This procedure was normally continued until all dirt and grime were removed. Following the bath, some time was usually spent in smoothing the hair. They seemed especially particular about the long tail, for when it became covered with mud or other material they would grasp it in the front feet and pass it back and forth through the mouth to remove the clinging particles. Only during the molt were they observed to appear rough and unkempt.

SIGNS

The presence of jumping mice can sometimes be detected by searching for certain characteristic signs. Concerning these rodents Bailey (1926) states, "To obtain the seeds of grass, on which they mainly sub-

sist, they cut off the tall stems as high up as they can reach, draw them down and cut them off again, and repeat this until the seed-laden tops can be taken. Little heaps of grass stems cut in sections about 3 inches long are found through the meadows where the jumping mice live and are unmistakable evidence of their presence, being always much longer than the grass cuttings of meadow mice and other short-legged species." Such signs have also been reported by Sheldon (1934) and Hamilton (1935).

During the present study it was observed that they quite frequently produce another type of "sign" by their feeding activities which is just as characteristic and often more easily found than that above. They do not consume all parts of a grass head, but allow certain portions to fall to the ground and form characteristic little piles containing seeds, and other parts of the spikelet such as the lemma, palea, glumes, and rachis. These were first noted while observing caged animals and were later seen on several occasions in the field, especially in the edge of timothy patches bordering marshy areas inhabited by these mice. To be reasonably certain that these piles were the work of jumping mice alone, several *Peromyscus* and *Microtus* were caged and given the same grass heads as jumping mice in other cages. In no instance were either observed to leave the "pile of debris" so characteristic of *Zapus*. If they utilized the heads at all, they cut them to shreds without removing the seeds and allowing the pile of debris to accumulate.

ENEMIES

No instance of predation on jumping mice was observed but two cases were supplied by Dr. W. H. Marshall as follows: A northern pike *Esox lucius*, collected in Itasca Park in the summer of 1946, contained an adult jumping mouse. In June, 1948, E. M. Sutton observed a weasel *Mustela* sp. at the Delta Waterfowl Research Station with a jumping mouse in its mouth. From these 2 observations and certain others reported in the literature, it seems safe to assume that jumping mice are preyed upon by representatives of all major vertebrate groups. Dearborn (1932) reported them as one of the prey species of mink. According to Hamilton (1935) Surface records *Zapus* from the stomach of a rattlesnake. Pearson & Pearson (1947) reported that *Z. hudsonius americanus* was one of the prey species of barn owls. Vergeer (1948) collected a green frog, *Rana clamitans*, which had swallowed a jumping mouse, *Z. hudsonius hudsonius*.

PARASITES

All jumping mice handled were examined for external parasites. They quite frequently harbored fleas of two species, *Megabothris quirini* and *Megabothris wagneri* (Identified by Dr. A. L. Burroughs) and occasionally a larval tick, *Dermacentor variabilis*. One snap-trapped specimen had a hole in the throat region from which a bot-fly presumably emerged. Three others had such holes in the inguinal region. Hamilton (1935) reports having found a louse on a *Zapus*, and Sheldon (1938) reports find-

ing a number infested by larva of the bot-fly, *Cuterebra fontinella*. Erickson (1938) examined 18 *Zapus hudsonius* and found 3 to be parasitized. Nematodes of the genera *Subulura* and *Spirocera*, a dipterous larva *Cuterebra* sp., and a fluke of the genus *Notoctylus* were found.

HABITAT PREFERENCE

During 1941, 1946, and 1947 extensive small mammal trapping was done during the periods when jumping mice were known to be active. A total of 24,959 trap nights (exclusive of those at Itasea and Centerville where the jumping mice were marked and released for home range studies) were completed in Carlton, Clearwater, Ramsey, and Anoka Counties, Minn. and Barron and Rusk Counties, Wis. Included are 975 trap nights of University of Minnesota forestry students at Cloquet Forest Experiment Station in Carlton County. Both "live" and snap-traps were used but the data are comparable since those caught in live-traps were removed from the areas. During the earlier trapping periods, no particular vegetative type was given preference in the selection of trapping areas but later, the types most likely to yield jumping mice were more frequently trapped. Sufficient data for comparison were obtained in all cases. No general type was trapped less than 947 trap nights (Table 3). By reducing the data to the number caught per 100 trap nights, a quantitative comparison of the relative numbers found in the various communities was made.

No effort is made to describe the various communi-

TABLE 3. The relative abundance of jumping mice in various vegetative types as determined by trapping.

Vegetative Type	Trap Nights	No. Caught	No. Per 100 Trap Nights
Upland Deciduous Forest.....	1,841	4	.22
Aspen.....	650	1	
Aspen-White Birch.....	246	1	
Oak (Red, White, Bur).....	945	2	
Upland Coniferous Forest.....	1,021	0	0
Jack Pine.....	443		
Norway Pine.....	508		
Norway Pine-Jack Pine.....	48		
Norway Pine-White Pine.....	22		
Upland Deciduous-Coniferous Forest.....	947	3	.32
Birch-Norway Pine-Jack Pine.....	240		
Birch-Aspen-Norway Pine-Jack Pine.....	122		
Birch-Aspen-Norway Pine-Jack Pine-White Pine.....	414	1	
Aspen-Jack Pine.....	73	1	
Aspen-Birch-Jack Pine.....	98	1	
Coniferous Swamp.....	1,168	4	.34
Black Spruce-Tamarack.....	1,037	1	
Tamarack-White Cedar-Balsam.....	33		
Balsam-White Cedar-Black Spruce.....	25	1	
Black Spruce-Balsam.....	40		
Balsam-White Cedar.....	24	2	
Willow-Alder.....	6,252	45	.72
Grass and/or Sedge Meadow.....	13,730	66	.48
Total.....	24,959	122	.49

ties comprising the areas trapped since it is desired only to point out the general types in which these rodents occur. The areas trapped are designated according to their general type as upland deciduous forests, upland coniferous forests, upland deciduous-coniferous forests, coniferous swamps, willow-alder thickets, or grass and/or sedge meadows. In some instances the distinction between the latter 2 was quite arbitrary since it was not possible to state whether the shrub stage had superseded the preceding one. The types trapped, number of trap nights, number of jumping mice caught, and number caught per 100 trap nights are summarized in Table 3.

Jumping mice were caught in all types trapped with the exception of upland coniferous forests. The greatest numbers .72 and .48 per 100 trap nights, were found in willow-alder thickets and grass and/or sedge meadows respectively. The distinction between these 2 was often an arbitrary one and for practical purposes they might be considered as belonging to the same life form. Coniferous swamps ranked next, .34 per 100 trap nights, followed by upland deciduous-coniferous forests .32, upland deciduous forests .22, and upland coniferous forests 0.

Jumping mice were found more commonly in the moist environs of the lowlands than in the more mesic uplands. Greater numbers were found in the more open type lowlands than in the forested types. These favored types normally bordered small streams or pot holes and afforded moist to semi-aquatic habitats (Fig. 9). Even in the more xeric types, a closer inspection usually revealed the presence of a small stream or pot hole close by. The preference of jumping mice for moist habitats has been pointed out by Preble (1899), Seton (1909), Howell (1924), Svihla & Svihla (1933), Borell & Ellis (1934), Davis (1934), Sheldon (1934), Blair (1940a) and others.

DESCRIPTION OF HABITAT

Data were presented which indicate that jumping mice prefer more or less moist and open habitats. Study plot 2 Centerville consisted largely of such types and supported moderately high populations (see populations). Certain areas within this plot are believed to be more or less typical of preferred habitats and are included in the following description.

The 25.25 acre plot is contained in the SE quarter of S27, T31N, R22W, 1 mile south and 1/4 mile west of Centerville, Anoka Co., Minn. For the most part the plot is within the NE 40 acres but it includes additional territory adjacent to the south and west borders. The geological history of the area dates to the Pleistocene. It is included in the Anoka Sandplain which was laid down as outwash sand during the retreat of the Grantsburg sublobe of the late Wisconsin ice age (see Cooper 1935). This forty is typical of the farms in that locality in that much of it is low and marshy and not suitable for cultivation. The surrounding uplands are well drained, and in general, intensively tilled. Corn, small grain, and hay plants constituted the principal cultivated crops in 1947. Two types of soil are found on the area. The soil of the uplands is a loamy fine sand designated as



FIG. 9. *Zapus* Habitat along Nicollet Creek, Itasca Park, Minn. This area supported 11 to 12 Jumping Mice per Acre during Aug., 1941. (Photo by Clyde Christenson).

Merrimac loamy fine sand by Smith *et al* (1918) and is described as "consisting of a brown to dark-brown loamy fine sand, 8 to 10 inches deep, underlain by a light brown to brown loamy fine sand which in many places continues into the substratum." In the low marshy areas the soil is described by Smith (1918) as peat, heavy subsoil phase "which consists of black sandy peat or muck, 10 to 18 inches deep, underlain by a grayish, clayey to fine sandy clay subsoil, which rests upon either a clayey or a fine sandy substratum."

The forty is bounded on the north by a well-travelled gravel road and on the east by an elevated, man-made prominence which covers an underground pipe line. To the south the cover and topography are more or less continuous. The west boundary is marked by a fence row, heavily grown with vegetation. Adjacent to the northern $\frac{3}{4}$ of this boundary is a wooded area of about 10 acres. The southern part (about 4 acres) is low and marshy and supports herbaceous as well as woody vegetation, while the remainder is a well drained upland. All of the low land and a part of the upland are included in study plot 2 (Fig. 10).

Approximately 560 feet from the NE corner of the forty a small stream, 4 to 6 feet wide, flows into the area meandering across it in a westerly direction. On reaching the western boundary, it turns abruptly to the north and flows off the area. During early summer (May and June) the stream was filled with water ranging in depth from 3 to 4 inches to about 1 foot. As the summer progressed, the stream became stagnant (July) and gradually "dried up" until, at the close of the summer (Aug.) no standing water remained. The lower portions of the stream bed remained moist throughout the entire season. Three man-made drainage ditches, each of which drains an outlying low marshy area, lead into the stream from the south. During May and early June

these ditches contained water but by July they were completely dry.

In general, study plot 2 consisted of the uncultivated land adjacent to the stream and its tributaries (see Fig. 10).

Six general vegetational types occurred on the plot: Low marshy areas with herbaceous vegetation, low marshy areas with woody and herbaceous vegetation, moist meadows, dry meadows, wooded uplands, and a transition area between the wooded uplands and low marshy areas. A short description of each follows.

Low Marshy Areas with Herbaceous Vegetation: All of this type occurred east of the fence row separating the NE forty from the wooded part of the plot (Fig. 10). In general, this type occupied the lower areas along the small stream but there were 4 outlying areas. During May and June all of these areas were partially filled with water but by July 15 all were dry save one. It, too, was dry Aug. 7. The following plants were the most common ones occurring in such situations: *Dryopteris Thelypteris*, *Onoclea sensibilis*, *Equisetum pratense*, *Typha latifolia*, *Sagittaria latifolia*, *Calamagrostis canadensis*, *Cyperus strigosus*, *Eleocharis palustris*, *Scirpus validus*, *Scirpus atrovirens*, *Carex scoparia*, *Carex vulpinoidea*, *Carex riparia*, *Carex retrorsa*, *Salix cordata*, *Polygonum pennsylvanicum*, *Spiraea alba*, *Impatiens biflora*, *Parthenocissus vitacea*, *Mimulus ringens*, *Veronica virginica*, and *Galium trifidum*.

Low Marshy Areas with Herbaceous and Woody Vegetation: All of this type with the exception of one small area occurred west of the fence row separating the NE forty from the wooded part of the plot (Fig. 10). It also was filled with water during May and June. In fact, small pools of water persisted in the larger area until about August 15. The most common plants of this type include: *Dryopteris Thelypteris*, *Sagittaria latifolia*, *Carex retrorsa*, *Salix cordata*, *Salix discolor*, *Alnus incana*, *Ranunculus pennsylvanicus*, *Caltha palustris*, *Penthorum sedoides*, *Ribes americanum*, *Spiraea alba*, *Rubus strigosus*, *Impatiens biflora*, *Parthenocissus vitacea*, *Epilobium adenocaulon*, *Cicuta bulbifera*, *Verbena hastata*, *Mimulus ringens*, *Plantago major*, *Galium trifidum*, *Eupatorium perfoliatum*, and *Solidago canadensis*.

Moist Meadows: This type occurred commonly along the small stream, drainage ditches, and low marshy areas. In general, it remained moist so long as the lower adjoining areas contained water but was sufficiently drained to prevent standing water except during extremely wet weather. The most common plants include: *Equisetum pratense*, *Echinochloa crusgalli* Var. *longiseta*, *Phleum pratense*, *Spartina pectinata*, *Poa palustris*, *Cyperus strigosus*, *Eleocharis palustris*, *Lilium Michiganensis*, *Rumex mexicanus*, *Rumex Acetosella*, *Polygonum pennsylvanicum*, *Chenopodium album*, *Amaranthus retroflexus*, *Ranunculus pennsylvanicus*, *Thalictrum dasycarpum*, *Potentilla norvegica*, *Rubus strigosus*, *Rosa blanda*, *Medicago lupulina*, *Vicia americana*, *Euphorbia corollata*, *Acer Negundo*, *Viola* sp., *Oenothera biennis*, *Cicuta maculata*, *Asclepias incarnata*, *As-*

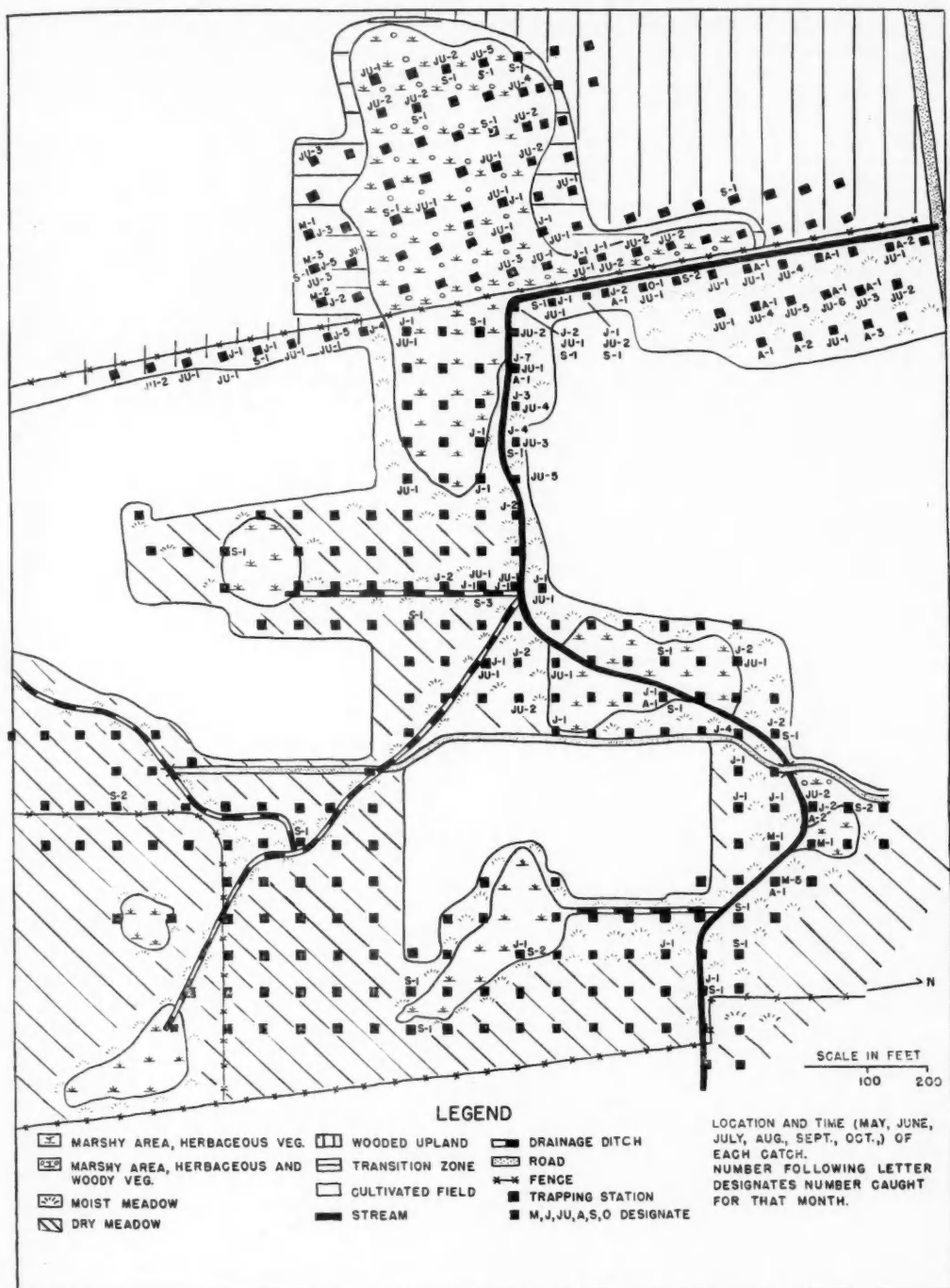


FIG. 10. Map of Plot 2 Centerville, Minn., showing general vegetational types, location of trapping stations, and stations where jumping mice were caught.

clepis syriaca, *Convolvulus sepium* Var. *americanus*, *Phlox pilosa*, *Verbena hastata*, *Stachys palustris*, *Castilleja coccinea*, *Plantago major*, *Galium boreale*, *Eupatorium perfoliatum*, *Solidago canadensis*, *Eriogon philadelphicus*, *Erigeron ramosus*, *Antennaria plantaginifolia*, *Heliopsis helianthoides* Var. *scabra*, *Rudbeckia hirta*, *Achillea lanulosa*, *Senecio Balsamitae* Var. *pauperculus*, *Sonchus arvensis* Var. *glabrescens*, and *Hieracium canadense*.

Dry Meadows: This type occupied the well drained, uncultivated uplands east of the fence separating the NE forty from the wooded part of the plot. At no time were these areas moist except following precipitation. The most common plants include: *Echinochloa crusgalli*, *Echinochloa crusgalli* Var. *longisetia*, *Setaria lutescens*, *Agropyron repens*, *Chenopodium album*, *Amaranthus retroflexus*, *Rorippa islandica* Var. *microcarpa*, *Trifolium hybridum*, *Melilotus officinalis*, and *Ambrosia artemisiifolia*.

Wooded Uplands: Included in this type is the southern part of the fence row separating the wooded and unwooded parts of the plot as well as the wooded upland previously mentioned. The most common plants include: *Corylus americana*, *Quercus macrocarpa*, *Quercus borealis*, *Prunus pennsylvanica*, *Prunus americana*, *Polygala sanguinea*, *Acer Negundo*, and *Sambucus pubens*.

Transition Area: A small band of this type occurred around the periphery of the large marshy area in the western part of the plot. The most common plants include: *Populus tremuloides*, *Betula papyrifera*, *Ulmus americana*, *Rosa blanda*, *Rhus hirta*, *Acer Negundo*, *Vitis vulpina*, *Cornus stolonifera*, *Cornus Baileyi*, and *Vaccinium pennsylvanicum*.

By trapping the plot from May to Oct. 1947, considerable data of a quantitative nature were compiled which supply information concerning choice of habitat. These data indicated that the amount of inhabited territory changed from time to time. The changes were correlated with the height of the water table. To a certain point, the amount of inhabited area was increased by the lowering of the water table but beyond this it had the opposite effect (discussed under population studies). An attempt is made to show the preferred habitats by months but the changes brought about by seasonal aspects seriously impair the value of such data. For example, a cat-tail marsh might be filled with water in May but completely dry in Aug. Nevertheless, the recording of the general type in which each catch was made provided a certain degree of quantitative information relative to habitat preference.

A total of 12,330 trap nights was completed at the 310 trapping stations (Fig. 10) during May, June, July, Aug. and Sept. (Table 4). Live traps were used during all months except Sept. when snap traps were used. Two hundred and fifty-six (256) individual catches were made as shown on Fig. 10 and summarized in Table 4. The data have been reduced to number of catches per 100 trap nights for quantitative comparisons.

TABLE 4. Showing the number of trap nights, number of catches of jumping mice, and number of catches of jumping mice per 100 trap nights in each general vegetational type on study plot 2 Centerville, Minn., 1947. (May, June, July, and Aug.—live traps, Sept.—snap-traps.) (Includes one which does not appear on Fig. 10—Moist Meadow, July. Does not include the one caught in Oct. shown on map.)

	MAY			JUNE			JULY		
	No. Trap Nights	No. of Catches	No. Per 100 Trap Nights	No. Trap Nights	No. of Catches	No. Per 100 Trap Nights	No. Trap Nights	No. of Catches	No. Per 100 Trap Nights
Marshy Area..... (Herbaceous vegetation)	36	1	2.78	195	6	3.08	273	2	.74
Marshy Area..... (Herbaceous and Woody vegetation)	0	0	80	6	7.50	522	38	7.28
Moist Meadow.....	123	6	4.88	1029	43	4.18	1117	58	5.19
Dry Meadow.....	18	0	0	147	0	0	382	0	0
Transition.....	144	6	4.17	132	14	10.61	241	8	3.28
Wooded Upland.....	36	0	0	58	7	12.07	306	6	1.96

	AUGUST			SEPTEMBER			TOTAL		
	No. Trap Nights	No. of Catches	No. Per 100 Trap Nights	No. Trap Nights	No. of Catches	No. Per 100 Trap Nights	No. Trap Nights	No. of Catches	No. Per 100 Trap Nights
Marshy Area..... (Herbaceous vegetation)	381	1	.26	610	6	.98	1495	16	1.07
Marshy Area..... (Herbaceous and Woody vegetation)	530	2	.38	880	7	.79	2012	53	2.63
Moist Meadow.....	1014	16	1.58	1730	16	.92	5013	139	2.77
Dry Meadow.....	545	0	0	790	3	.38	1882	3	.16
Transition.....	183	0	0	270	2	.74	970	30	3.09
Wooded Upland.....	238	0	0	320	2	.62	958	15	1.56

Certain vegetational types were favored during all months except Sept. but the favored type was not consistently the same from month to month. All types except dry meadows and transition areas were favored during at least one month and one of these, transition areas, was favored for the season as a whole. In May moist meadows were favored, in June wooded uplands, in July marshy areas with herbaceous and woody vegetation, in Aug. moist meadows, and in Sept. marshy areas with herbaceous vegetation (but not markedly). These data suggest that the vegetational type alone is not the controlling factor in determining the presence of these mice or that their preference for vegetational types differ from month to month.

For the entire season the mice were caught most commonly in the vegetational types in the following order: transition areas, moist meadows, marshy areas with herbaceous and woody vegetation, wooded uplands, marshy areas with herbaceous vegetation, and dry meadows. These data suggest that jumping mice prefer a moist habitat since the most xeric type was the least preferred and the 3 favored types are more or less mesic. Even so, this suggestion is not entirely

consistent since wooded uplands were preferred to marshy areas with herbaceous vegetation.

Thus far the analysis of the data has been of a general nature and has not considered the seasonal changes which occurred on the area. A more thorough investigation of each type by month reveals some important aspects heretofore unconsidered.

Marshy Areas with Herbaceous Vegetation: Only during Sept., when .98 mice per 100 trap nights were caught, did this type rank first as a favored habitat. During the remainder of the season it ranked relatively low. For May, when such areas were largely filled with water, it ranked 3rd (2.78 per 100 trap nights). During June when the water table was somewhat lower it was 5th (3.08). For July when such areas were largely dry it remained 5th (.74) and in Aug. it was third (.26). Nothing in particular is indicated except these mice were not particularly fond of such areas (the data for Sept. being disregarded since they are not considered significant as later discussed).

Marshy Areas with Herbaceous and Woody Vegetation: During May all of this type was filled with water, so much so, that none of it was trapped. During June a small portion of it was trappable and 7.50 mice per 100 trap nights were caught giving it third rank in preference. For July the marsh was largely devoid of standing water but moist and it ranked first (7.28). During Aug. this type became dry with only occasional damp spots but at the same time it was still more mesic than any area on the plot, save 1 (stream bed) and it was second (.38). For Sept. .79 mice per 100 trap nights were taken.

Moist Meadow: This type ranked consistently high throughout the summer, May 1st (4.88), June 4th (4.18), July 2nd (5.19), Aug. 1st (1.58), and Sept. 2nd (.92). The data for Aug. seem especially significant for this was the most critical month (see population studies) so far as numbers on the plot were concerned. The majority of catches for Aug. occurred in the moist meadow along the small stream in the NW part of the plot (Fig. 10). This particular part of the stream remained more moist during this period than any other part of the plot.

Dry Meadow: This was the most xeric type on the plot. No mice were caught except during Sept., .38 per 100 trap nights.

Transition Area: During May and June, when the adjoining marsh was filled with water this was one of the favored types ranking second for both months (4.17 and 10.61 respectively). During July when the marsh was "drying up," the number of catches decreased (3.28) and during Aug., when the marsh was dry, no mice were caught. For Sept. .74 per 100 trap nights were trapped.

Wooded Uplands: During May no jumping mice were taken in this type but too few trap nights (36) were completed for conclusions. For June more mice were caught per trap night than in any other type (12.07). All were trapped in the wooded fence row south of the large marsh in the western part of the plot which was largely filled with water (Fig. 10). For July only 1.96 per 100 trap nights were caught

in this type and all catches were again in the wooded fence row. The marsh was largely dry during this month. During Aug. when the marsh was dry, no mice were taken in wooded uplands. For Sept. .62 mice per 100 trap nights were caught in wooded uplands and for the first time 1 was taken in the extensive woods north of the marsh.

The data clearly indicate that this mouse preferred the environs at the periphery of standing water or damp areas during May, June, July, and Aug. In all types, for which the mice showed a preference, the number caught per 100 trap nights was definitely influenced by its nearness to water. For this group, the vegetational type seemed of secondary importance while its location with respect to water seemed of greater importance.

The fact that marshy areas with herbaceous vegetation at no time ranked high during these months indicates that the vegetational type is also of importance. This type on the basis of exposed moist surfaces in the immediate vicinity of water should have ranked high during all months save Aug. but this was not the case.

It seems, therefore, that jumping mice prefer certain vegetational types during these months but these types must be near water. Although these mice undoubtedly are not strictly aquatic several observations attest to the fact that they do not hesitate to enter the aquatic environs near which they live. On June 12 one was caught in a trap which was entirely surrounded by water 1 to 2 inches deep. The trap was set on a clump of sedge which extended 2 inches or so above the water (Fig. 11). The nearest dry land was 20 feet away but there were numerous other clumps spaced in such a way that a jumping mouse could possibly have gained access to the trap without entering the water but this possibility seems unlikely. This mouse, like others at various times, went into the marsh when released to escape. On June 24 an-



FIG. 11. Live-trap on Clump of Sedge about twenty feet from Dry Land in Study Plot 1, Centerville, Minn. A Jumping Mouse was caught in this trap June 12, 1947. (Photo by Author.)

other was caught under similar conditions. Preble (1944) observed a jumping mouse swimming in a lake but concluded that its presence there was due to the activity of a dog hunting along the shore. Dr. W. H. Marshall found a jumping mouse in the stomach of a Northern Pike, *Esox lucius*, collected in Itasca Park in 1946.

For Sept. the mice did not show a marked preference for moist areas. They were widely scattered over the area and were fairly common in all types (Fig. 10, Table 4). They were caught for the first time in dry meadows and the extensive upland woods. These facts indicate they were inclined to shift around considerably during this month. Although no data are available to support such an assumption, it seems that these movements were associated with the hibernating habits of the animal. During this period they doubtless seek suitable hibernating sites and the fact that they were found in the more elevated areas is suggestive that they seek the better drained spots for hibernation. Nicholson (1937) reports that a hibernating jumping mouse was found Oct. 20, 1936 in a sand bank. The nearest marshy meadow was about 100 yards distant. Two jumping mice were taken in 1935 in a large marsh some distance away, and approximately 35 feet lower in elevation.

MAMMALIAN ASSOCIATES

Other mammals caught on the area included: Cinereous Shrew, *Sorex cinereus cinereus* 60; Black-backed Shrew, *Sorex arcticus laricorum* 7; Short-tailed Shrew, *Blarina brevicauda brevicauda* 73; Short-tailed Weasel, *Mustela erminea bangsi* 2; Striped Ground Squirrel, *Citellus tridecemlineatus tridecemlineatus* 40; Gray Chipmunk, *Tamias striatus griseus* 8; Mississippi Valley Pocket Gopher, *Geomys bursarius bursarius*; Prairie White-footed Mouse, *Peromyscus maniculatus bairdii* 140; Wood mouse, *Peromyscus leucopus noveboracensis* 4; Pennsylvania Meadow Mouse, *Microtus pennsylvanicus pennsylvanicus* 250, and House Mouse, *Mus musculus* 4. Other mammals known to occur on the area were: Raccoon, *Procyon lotor hirtus* and Striped Skunk, *Mephitis mephitis* subsp.

The three shrews, short-tailed weasel, and meadow mouse were found most commonly in the same types as the jumping mouse. The short-tailed weasel was doubtless a predator on jumping mice. The short-tailed shrew could be considered as a potential predator but its chances of catching a jumping mouse would seem poor. What relationship existed between the other 3 and the jumping mouse is unknown. The prairie white-footed mouse and striped ground squirrel were quite common in the dry meadows. The former was also common in the cultivated fields. The ranges of these two overlapped that of the jumping mouse in the transition areas between dry and moist meadows. The gray chipmunk and wood mouse were found only in the wooded uplands. Their ranges overlapped that of the jumping mouse in the transition area between wooded upland and low marshy area. The pocket gopher was found in the dry meadows and at the edge of cultivated fields. The feral house mice doubt-

less emigrated from the nearby farm buildings. The raccoons ranged widely over the area but chiefly along the small stream and marshy areas. They frequently visited the corn fields where they fed on the ears. A skunk was seen in the dryer upland meadow.

HOME SITES

Observations in the field and of caged animals supplied information on the choice of home sites. Burrows and nests were most difficult to locate in the field. The few reported as found under natural conditions, were located more or less by accident.

Captives characteristically constructed oval grass nests of various sizes. Some were on the surface, others underground.

The description of the home sites found in the field follow: On Aug. 7, 1941 in Itasca Park, Minn., a jumping mouse was observed near a clump of sedge bent over to form a dense mat with a diameter at the base of 1 foot and about the same height. Under the overhang was an oval grass nest. It closely resembled the nests built by captives. Although the jumping mouse was not seen to either enter or leave the nest, the writer thought it was its home site. This assumption is supported by the reports of others. Preble (1899) states: "During the latter part of summer *Zapus* makes a globular nest of grass about 4 inches in diameter, with a small entrance at the side." Bailey (1926) reports that *Z. h. campestris* makes summer homes on the surface of the ground. According to him, they are "neat little balls of fine grass with a tiny opening at one side and a soft lining in the central chamber." He further states that they are well concealed under grass and other vegetation. Borrell & Ellis (1934) indicate that jumping mice live in globular nests on the surface of the ground in tall grass. Hamilton (1935) records 2 nests found in New York. One was composed of leaves and a few grasses under a rotten log. The other was in a tussock of grass above ground level. Sheldon (1938) says that *Zapus* live, during the summer, in above-ground nests built in open meadows. She includes a description of these nests.

Aug. 9, 1941 the late Russel M. Berthel and George Rysgaard found the nest of a jumping mouse containing 6 young, 6 miles east of Emmons, Freeborn Co., Minn. They supplied the following details. The nest was in the center of a very rotten willow log, about 3 feet in diameter. It was lined with small pieces of pulpy wood and the runway to the nest was open at both ends.

Mr. Karl W. Kahmann of Hayward, Wis. found the nest of a jumping mouse in that locality containing 5 young about July 28, 1941. Concerning this nest he wrote, "... they (the young) were taken from a nest placed at ground level on the inside of a large red oak, which, while living is rotted to a shell of about 4 inches thick and is open for a distance of at least 10 feet high and 18 inches wide, facing north. The tree has a diameter of about 2 feet at stump height.

"The nest was sunken among the rotted wood and debris at the ground and was composed of grasses,

plant fibers, and rootlets, and was a globular structure about 6 inches in diameter with an indefinite entrance hole near the top.

"The parent (one of them) was in the nest and left when disturbed."

Mr. Kahmann further stated, "I would say that this nest was rather unusual as to location and have found several while plowing our garden, of similar construction but underground at a depth of about 6 inches from the top of the nest."

Sheldon (1938) reports that Wendell P. Smith dug up a nest of jumping mice located in a potato hill some 3 or 4 inches below the surface. Ivor (1934) records the nest of a jumping mouse, with 5 young, found in a humus deposit in Ontario. York (1945) reports that a tractor plowed up a nest of meadow jumping mice containing a female and 6 large young in Canada. The nest was made of grass and was not more than 3 inches below the surface.

On Aug. 16, 1947 Buddy Cardinal of Centerville, Minn., was poking in a hollow root (Fig. 12) located on Plot 1, Centerville. He saw a jumping mouse and informed the writer. An investigation revealed that the root contained the nest of a jumping mouse with 5 young (Fig. 13). The root had become detached from the base of a large willow and was exposed above ground for a distance of about 4 feet. At the proximal end it was about 10 inches in diameter and tapered to about 3 inches in 4 feet. Only the exposed portion of the root was hollow, the cavity measuring $4\frac{1}{2}$ by 6 inches at the proximal end and tapered to 1 inch at the distal end. The large end was entirely plugged with dirt and debris when found. At the other end, a mouse-size hole entered from the side. This hole had been much used as evidenced from its smooth appearance and the well-worn trail leading to it. Eighteen inches from the proximal end was a flimsy nest amounting to nothing more than a pile of wood pulp and the leaves of oaks



FIG. 13. Young Jumping Mice in hollow root where nest was located (Fig. 12). (Photo by H. L. Gunderson.)

and grasses. The pile was 4 inches in diameter and $\frac{1}{2}$ inch high.

No hibernating sites were found in the field. Captives were observed to hibernate in underground grass nests. Preble (1899) states that hibernating jumping mice are generally found in nests in holes varying from a few inches in depth to 2 or 3 feet below ground surface. Nicholson (1937) found a hibernating jumping mouse in a sloping sand bank. The mouse was in a simple nest, made of a few elm leaves, at a vertical depth of 2 feet 3 inches and a horizontal depth of 3 feet 9 inches.

These data indicate that jumping mice almost invariably construct a nest usually of grass and/or leaves which they use as a home site. The nest is generally located in a protected spot such as a hollow log, hollow tree, under some protecting object, or underground.

DATE OF EMERGENCE FROM HIBERNATION

The date of emergence was determined for 1941, 1942, 1947, and 1948 by continually trapping favorable habitats in the spring until jumping mice began to appear in the catch. In 1941 the trapping was at Cloquet, Carlton Co., Minn., from April 1 until the date of emergence of both males and females which occurred about May 2 and 26 respectively. For 1942 the trapping was also at Cloquet and began on April 16. A male was caught on May 16 but no female was taken by May 21 when trapping was discontinued. Areas in the vicinity of St. Paul, Ramsey Co., and Centerville, Anoka Co., were trapped from April 19 in 1947. The first male was caught May 13 and the first female May 25. In 1948 the Centerville area was trapped beginning April 27. The first male was taken April 29. The date of emergence of the females was not determined since no traps were out during May but 3 were taken the night of June 1 when trapping was resumed.

The data reveal 2 facts. First, the males were active before the females for all 4 years (1941, 24

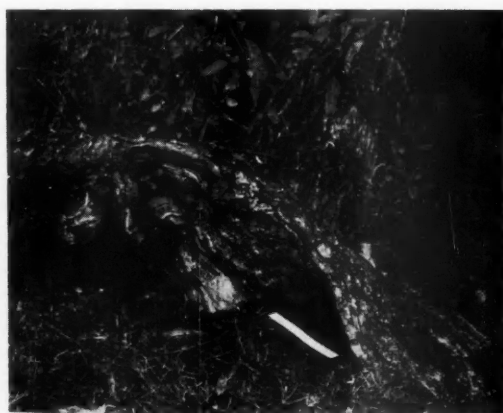


FIG. 12. Proximal end of hollow root in which a Jumping Mouse Nest was found on Study Plot 1, Centerville, Minn., Aug. 16, 1947 by Buddy Cardinal. (Photo by H. L. Gunderson.)

TABLE 5. Occurrence of some phenological events with reference to the date of emergence of the jumping mouse from hibernation in the same areas. Observers:—A. C. H., A. C. Hodson; W. H. M., W. H. Marshall; R. M. B., R. M. Berthel; D. Q., Don C. Quimby. Localities:—Ce., Centerville, Minn.; Cl., Cloquet, Minn.; P. C., Pine City, Minn.; S. P., Saint Paul, Minn.

Event		Date by	Locality	Observer	Days preceding emergence of ♂ jumping mice, at least
BIRDS					
Lesser Scaup Ducks arrive		3/26/48	S.P.	D.Q.	34
Red-Winged Blackbirds arrive		3/29/47	S.P.	A.C.H.	45
		4/ 5/41	Cl.	D.Q.	27
Robins arrive		3/29/47	S.P.	A.C.H.	45
		4/ 2/41	Cl.	D.Q.	30
Shoveller Ducks arrive		3/31/48	S.P.	D.Q.	29
Meadowlarks arrive		4/ 1/47	S.P.	A.C.H.	42
Red-Breasted Nuthatches arrive		4/ 7/41	Cl.	R.M.B.	25
Eastern Fox Sparrows arrive		4/ 8/41	Cl.	D.Q.	24
Eastern Ruby-Crowned Kinglets arrive		4/ 9/41	Cl.	D.Q.	23
		4/19/47	S.P.	A.C.H.	24
Mallard Ducks arrive		4/11/48	S.P.	D.Q.	18
Bluebirds common		4/28/47	S.P.	A.C.H.	15
Flickers common		4/28/47	S.P.	A.C.H.	15
Brown Thrashers common		4/30/47	S.P.	A.C.H.	13
Myrtle Warblers arrive		4/30/47	S.P.	A.C.H.	13
Pheasants Nesting		5/ 9/47	Ce.	W.H.M.	4
Wilson's Snipe Nuptial Flight		5/ 9/47	Ce.	D.Q.	4
White Throated Sparrows arrive		5/10/47	S.P.	A.C.H.	3
House Wrens arrive		5/12/47	S.P.	A.C.H.	1
Baltimore Orioles arrive		5/12/47	S.P.	A.C.H.	1
MAMMALS					
Pocket Gophers active (mounds)		4/ 1/48	S.P.	D.Q.	28
Moles active (burrows)		4/ 1/48	S.P.	D.Q.	28
Striped Ground Squirrels emerge from hibernation		4/ 1/41	P.C.	D.Q.	31
		4/ 1/47	Ce.	D.Q.	42
		4/ 1/48	S.P.	D.Q.	28
Woodchucks emerge from hibernation		4/ 5/41	Cl.	D.Q.	27
Western Chipmunks (<i>Eutamias</i>) emerge from hibernation		4/ 5/41	Cl.	D.Q.	27
		4/16/42	Cl.	D.Q.	30
Snowshoe Hares turning brown		4/11/41	Cl.	D.Q.	21
		4/13/42	Cl.	D.Q.	33
Eastern Chipmunks (<i>Tamias</i>) emerge from hibernation		4/18/41	Cl.	D.Q.	14
		4/13/42	Cl.	D.Q.	33
Snowshoe Hares in summer pelage		4/21/41	Cl.	D.Q.	11
		4/22/42	Cl.	D.Q.	24
INSECTS					
Canker Worms emerge		3/31/47	S.P.	A.C.H.	43
PLANTS					
Elderberry	Buds showing green tips	4/ 3/47	S.P.	A.C.H.	40
	Flower buds visible	4/13/47	S.P.	A.C.H.	30
	Leaves unfolded	5/ 2/47	S.P.	A.C.H.	11
		4/21/48	S.P.	A.C.H.	8
	Flower buds purple	5/ 4/47	S.P.	A.C.H.	9
		4/16/48	S.P.	A.C.H.	13

Table 5 continued.

Event		Date by	Locality	Observer	Days preceding emergence of ♂ jumping mice, at least
Soft Maple	Buds swollen	4/ 3/47	S.P.	A.C.H.	40
	Buds open	4/ 9/47	S.P.	A.C.H.	34
	In bloom	4/15/47	S.P.	A.C.H.	28
	Leaf buds expanded	5/ 2/47	S.P.	A.C.H.	11
		4/18/48	S.P.	A.C.H.	11
	Leaves unfolding	5/10/47	S.P.	A.C.H.	3
		4/23/48	S.P.	A.C.H.	6
American Elm	Flower buds swollen	4/ 3/47	S.P.	A.C.H.	40
		4/ 6/48	S.P.	A.C.H.	23
	Bud enlarged—tip red	4/20/47	S.P.	A.C.H.	23
		4/10/48	S.P.	A.C.H.	19
	Flower buds breaking	4/25/47	S.P.	A.C.H.	18
	In bloom	4/28/47	S.P.	A.C.H.	15
		4/12/48	S.P.	A.C.H.	17
	Leaf buds green, swollen	5/ 2/47	S.P.	A.C.H.	11
		4/16/48	S.P.	A.C.H.	13
	Leaves breaking	5/12/47	S.P.	A.C.H.	1
		4/23/48	S.P.	A.C.H.	6
		5/12/47	S.P.	A.C.H.	1
	4/30/48	S.P.	A.C.H.	—1	
Tamarack	Bud ends green	4/28/47	S.P.	A.C.H.	15
		4/16/48	S.P.	A.C.H.	13
	Buds expanded ½"	5/ 2/47	S.P.	A.C.H.	11
		4/21/48	S.P.	A.C.H.	8
	Leaf bundles ¼"	5/10/47	S.P.	A.C.H.	3
		4/24/48	S.P.	A.C.H.	5
Box Elder	Flower parts nearly fully extended	5/ 2/47	S.P.	A.C.H.	11
	Leaf buds opening	5/ 4/47	S.P.	A.C.H.	9
		4/16/48	S.P.	A.C.H.	13
	Leaves about 1"	5/10/47	S.P.	A.C.H.	3
		4/24/48	S.P.	A.C.H.	5
Ash	Flower buds swollen	5/ 2/47	S.P.	A.C.H.	11
	Flowers breaking out of buds	5/10/47	S.P.	A.C.H.	3
		4/23/48	S.P.	A.C.H.	6
	Leaf tips appearing	5/10/47	S.P.	A.C.H.	3
	Flowering	5/12/47	S.P.	A.C.H.	1
	Leaves breaking	5/12/47	S.P.	A.C.H.	1
		4/30/48	S.P.	A.C.H.	—1
Basswood	Buds swollen, green	5/ 4/47	S.P.	A.C.H.	9
		4/24/48	S.P.	A.C.H.	5
	Leaf tips showing	5/12/47	S.P.	A.C.H.	1
		4/30/48	S.P.	A.C.H.	—1
Bur Oak	Buds swollen	5/ 4/47	S.P.	A.C.H.	9
		4/21/48	S.P.	A.C.H.	8
	Leaf tips breaking	5/10/47	S.P.	A.C.H.	3
		4/27/48	S.P.	A.C.H.	2

days; 1942, at least 5 days; 1947, 12 days; 1948, no more than 34 days). Bailey (1929) likewise found this to be true in Sherburne Co., Minn. During 1927 he trapped from April 15. The first male was caught May 2 and the first female May 23. This earlier emergence date of the males is probably associated with the breeding season. Most females are inseminated soon after emergence (see extent of breeding season). Second, the date of emergence varied considerably from year to year. The difference was 14 days for 1941 and 1942 at Cloquet and for 1947 and 1948 at Centerville. The date of emergence was 11 days earlier in 1941 at Cloquet, some 100 miles north, than at Centerville in 1947.

The emergence date occurred late in the season as compared to certain other phenological events (Table 5). Both robins and red-winged blackbirds were observed 45 days previous to the date of emergence in 1947 (all references refer to earliest emerging male). Lesser scaup ducks, shoveller ducks, meadowlarks, red-breasted nut-hatches, eastern fox sparrows, ruby-crowned kinglets, and mallard ducks were observed from 18 to 42 days previous to emergence during the years of observation. Bluebirds, flickers, and brown thrashers were common 2 weeks before emergence in 1947.

Other hibernating rodents were observed to be active long before the jumping mouse: striped ground squirrel, 31, 42, and 28 days respectively for 1941, 1947, and 1948; woodchuck, 27 days in 1941; western chipmunk, 27 (1941) and 30 (1942) days; eastern chipmunk, 14 (1941) and 33 (1942) days. Snowshoe hares were observed to be molting from white to brown 21 (1941) and 33 (1942) days previous to emergence and were observed in summer pelage 11 (1941) and 24 (1942) days previous. Fresh workings of moles and pocket gophers were noted 28 (1948) days before emergence of the jumping mouse.

Several plants, including soft maple and American elm, bloomed 2 to 4 weeks earlier than the emergence date. Elderberry, soft maple, American elm, tamarack, box elder, ash, basswood, and bur oak were all leafed out to some degree at the time of emergence.

The above notations attest to the fact that the jumping mouse continues the "winter sleep" far into the spring and does not venture from the winter retreat until after certain other organisms of the community have long since shaken the lethargy of winter. At the time when the events of nature leave no doubt as to the end of winter, this dainty rodent ventures out to become active in the community. This late emergence is somewhat more vividly expressed by the following coincidence. For 2 years, 1947 and 1948, the emergence date has coincided closely with the remark "everything popping" in Dr. A. C. Hodson's personal phenological record.

Some of the later phenological events which occurred at about the same time as the emergence of the jumping mouse included: the arrival of house wrens, Baltimore orioles, and white-throated sparrows; first nesting of pheasants; maturing of American elm seeds; and breaking and unfolding of the

leaves of soft maple, American elm, ash, basswood, and bur oak.

An examination of the plant events in Table 5, where data are recorded for both 1947 and 1948, reveals that the emergence date for both years was, in most cases, approximately the same when referred to these events. The flower buds of elderberry were purple 9 and 13 days before emergence for 1947 and 1948 respectively. The leaves of the soft maple were unfolding 3 (1947) and 6 (1948) days before emergence. The American elms bloomed 15 (1947) and 17 (1948) days before emergence and the bud ends of the tamarack were green 15 (1947) and 13 (1948) days previous to this event. The leaves of the box elder were 1 inch 3 (1947) and 5 (1948) days earlier and the opening of the flower buds of the ash occurred 3 (1947) and 6 (1948) days sooner. The buds of the basswood were swollen 9 (1947) and 5 (1948) days earlier whereas the buds of bur oak were swollen 9 (1947) and 8 (1948) days before the date of emergence. On the average, the plant events listed in Table 5 occurred 13+ days earlier in 1948 than in 1947 and the jumping mouse emerged 14 days earlier in 1948 than in 1947.

These data indicate that the date of emergence of *Zapus* can be predicted fairly accurately by observing the sequence of occurrence of other phenological events and comparing them with the dates of their occurrence in previous years. This principle was recently pointed out by Leopold & Jones (1947). In 1948 the writer was able to predict, within a few days, the approximate time that traps should be put out in order to catch the earliest emerging jumping mice. The traps were put on April 27 and jumping mice were caught April 29. The knowledge gained during 3 previous seasons made this possible.

RELATIONSHIP BETWEEN WEIGHT AND DATE OF HIBERNATION

During 1946, 19 jumping mice were caged between July 19 and Sept. 20. The cages were kept in a screened building, subject to outside temperatures, until Oct. 16. From Aug. to the latter date the mice were observed and weighed periodically to determine the relationship between weight and date of hibernation. Entrance into hibernation was gradual. The mice became less active and were often observed in a drowsy, lethargic condition gradually grading into complete torpor. Certain periods of "hibernation" were of short duration. All of the cages contained soil, ranging in depth from 2 or 3 inches to about 2 feet, permitting the mice to burrow. This made observations difficult, particularly in the cages with the greater depths of soil. Nevertheless, the mice were "dug out" periodically and examined. Another method of detecting periods of inactivity was determining whether the food and water had been sampled. Weight trends were also good indices. An animal showing a marked weight loss late in the study was always suspected of having been in hibernation regardless of its condition at the time of examination. Those showing marked gains were not suspected of inactivity. The reasons are discussed

later. It was possible in all instances to determine the approximate date of hibernation. There was considerable difference even for mice in the same cage.

To define the causes of this intricate physiological process is beyond the scope of this paper but the data reveal that the relationship of body weight to the date of hibernation cannot be disregarded. The ratio, amount of fat to normal body weight is unquestionably of great importance but in the absence of satisfactory standards of "normal" body weights, it is impossible to set up quantitative ratios expressing this relationship. By tracing the weight changes previous to, during, and after hibernation it was possible to correlate these changes with the approximate date of hibernation for a given individual. The histories of various individuals, living under the same conditions, provided material for comparison relative to these 2 factors.

Eight entered into hibernation between Sept. 17 and Oct. 1, while the others had shown no tendency to hibernate by this date. The average weight of the hibernating group was 26.44 grams (22.8 to 28.6) as of Sept. 17, whereas that of the non-hibernating group was 16.06 grams (11.4 to 20.9). The hibernating group averaged 10.38 grams more than the non-hibernating group, a huge difference for such small animals. All of the early hibernating group were caged fairly early and, although 3 were subadults as of the date of caging, all could be considered adults (see development of young). The average length of captivity to Oct. 1 was 54 days (28 to 74). The rate of gain was greatly accelerated during the two-week period, Sept 3 to 17, previous to the two-week period when they entered into hibernation. The average daily change per mouse previous to Sept. 3 was $-.02$ grams, whereas the average daily change during the two-week period, Sept. 3 to 17 was $+.65$ grams. The two-week period, Sept. 17 to Oct. 1, when all entered into hibernation, was marked by weight losses for all (average $.26$ grams per day).

Seven that had shown no tendency to hibernate by Oct. 1 had entered into hibernation by Oct. 16. The average weight previous to hibernation was 23.44 grams (19.9 to 26.3). The average weight of the 4 non-hibernating mice was 19.42 grams (17.3 to 21.8) as of Oct. 10. For this hibernating group, the average length of captivity to Oct. 1 was 27 days (11 to 47). This group gained weight from the outset, but the greatest gains occurred during the two-week period, Sept. 17 to Oct. 1, previous to the two-week period when all entered into hibernation. The average gain per mouse per day was $.18$ grams previous to Sept. 17 but during the two-week period, Sept. 17 to Oct. 1, it was $.30$ grams. Five were weighed on Oct. 10. The 3 that had not entered into hibernation by this date were continuing to gain ($.13$, $.07$, and $.80$ grams per day), whereas the 2 that had entered into hibernation showed a loss in weight ($.26$ and $.21$ grams per day). Two, subadults as of the 15 and 16 of Aug. when caged,

entered into hibernation before any of the others, all adults.

The 4 that had not shown signs of hibernating by Oct. 16 were moved to a heated room on this date. Except one, accidentally killed on Oct. 24, these mice were observed to hibernate in the heated room. Inasmuch as the conditions were quite different after Oct. 16, no attempt was made to compare this group with the others so far as weight was concerned except for the period when they were in the unheated room. The average length of captivity to Oct. 1 was 17 days (16 to 19). Previous to Sept. 17 the average gain per mouse per day was $.02$ grams but during the 16 day period, Sept. 17 to Oct. 3, it was $.17$ grams. During the seven-day period, Oct. 3 to 10, it was $.45$ grams. The rapid gains during the latter period suggest that these mice would have entered into hibernation within a few days had they been allowed to remain in the unheated room. The change in surroundings doubtless retarded this process since the 3 that lived long enough to hibernate were observed to do so on Nov. 2, 8, and 12. Three were judged to be subadults as of Sept. 15 while the remaining one was an adult.

Regardless of other conditions, these data indicate that the mice exhibiting marked weight gains early in the season entered into hibernation before those that did not. The mice of the early hibernating group were heavier on the average at the time of hibernation than were those that hibernated at a later date. In general, the pattern of weight changes with reference to the date of hibernation were similar for all individuals. The two-week period previous to the approximate date of hibernation was marked by excessive gains in weight. Previous to this time the weight changes ranged from moderate losses to moderate gains. Excessive weight losses were noted for the few days following hibernation. No difference was noted in the time of hibernation for subadults of early litters as compared to that of adults. Subadults from late litters, and adults which for some reason failed to become obese at an early date, were the last to hibernate.

Observations in the field support the data from captives. All jumping mice taken after Sept. 20, 1941, 1946, and 1947 were either subadults or adults that were not fat. Fourteen, of 18, were young of the year and 4 were adults. Two of the adults had recently suckled young and another was in an emaciated condition. The average weight of the 13 weighed was 15.94 grams (10.5 to 20) which is considerably less than the average weight for those observed to hibernate in captivity.

It seems evident that the amount of body fat is of great importance in determining the date of hibernation. Others have reported similar conclusions. Wade (1930) reports, from his study of ground squirrels, that all animals that aestivated in summer in captivity were fat. The few wild squirrels captured in Oct. were not fat and were probably young ones that had not had sufficient time to grow and also acquire fat. Johnson (1931) states that fatness has

been agreed upon as a cause of hibernation by practically all who have studied this phenomenon. Hamilton (1934) believed that the accumulation of necessary fat is a contributing cause, if not the paramount reason, for hibernation of the woodchuck. He observed that young woodchucks of the year are always the last too be abroad in the fall. Hamilton (1935) observed that the heaviest jumping mice, *Napaeozapus*, were the first to hibernate among captives. He further reports that all late records were of animals, usually immature, that did not exhibit a layer of fat when skinned.

FOOD HABITS

A food preference study was conducted with caged animals in 1947. Throughout the summer various plants and invertebrates were collected on the Centerville study areas and made available to the captives along with the usual rations of oatmeal, prepared rat and mouse concentrate, various grains, grass heads, apple, et cetera. Although the numbers of different species used are by no means exhaustive, they seemingly represent a fairly reliable sample of the different types found on the areas. It was not possible to offer all simultaneously because of the difference in times of fruiting or emergence. No particular plant or insect can be designated as representing the favored food. By recording the degree of utilization of each some conclusions regarding the general choices can be made. For plants, utilization was designated as none, slight, moderate, or heavy. For insects these finer distinctions were unnecessary. If touched at all, they were generally totally consumed; i.e., with the exception of Lepidoptera wings and some heavily sclerotized areas. In some instances even these were partially consumed.

Forty species of plants as discussed, representing 20 families, were made available to the caged mice. In most cases (herbs) the entire plant was placed in the cage but in others (woody shrubs and lianas) only the ripened fruits with or without attached stems and leaves were made available. Only the fruits were utilized to any great extent. Only 2 cases of utilization of other plant parts were observed. The roots of *Typha latifolia* were slightly utilized and in view of Hamilton's (1935) report that a jumping mouse collected in a cattail swamp had the stomach filled with a starchy paste, perhaps the root stalk of *Typha*, it can be assumed that this also occurs under natural conditions. The leaves of a single species, *Setaria lutescens*, were the only ones observed to have been eaten. The degree of utilization was slight.

The dry indehiscent fruits of certain of the Gramineae *Setaria lutescens*, *Phleum pratense*, *Avena fatua*, *Agropyron repens* and the more or less fleshy fruits of some shrubs *Ribes Cynosbati*, *Ribes americanum*, *Fragaria* sp., *Rubus strigosus*, *Cornus stolonifera*, *Vaccinium pennsylvanicum* were heavily utilized. The dehiscent fruits of one of the legumes *Vicia americana* were also utilized heavily. These materials could possibly be classified as preferred foods.

TABLE 6. Utilization by caged jumping mice of various invertebrates collected in typical jumping mouse habitat.

Animal	Stage	Utilized
Gastropoda		
Snail.....		Yes
Slug.....		Yes
Arachnida		
Harvestman.....		Yes
Diplopoda		
Milliped.....		Yes
Orthoptera		
Green Katydid.....	Adult	Yes
Unidentified.....	Nymph	Yes
Field Cricket.....	Adult	Yes
Red-legged Locust.....	Adult	Yes
Unidentified.....	Nymph	Yes
Neuroptera		
Lacewing Fly.....	Adult	Yes
Ephemera		
May Fly.....	Adult	Yes
Odonata		
Dragon Fly.....	Adult	Yes
Hemiptera		
Squash Bug.....	Adult	Yes
Shield Back Bug.....	Adult	Yes
Unidentified.....	Adult	Yes
Homoptera		
Buffalo Tree Hopper.....	Adult	Yes
Coleoptera		
Ground Beetle.....	Adult	Yes
Carriion Beetle.....	Adult	No
Wire Worm.....	Larva	Yes
Lady Bug Beetle.....	Adult	No
Milk Weed Beetle.....	Adult	Yes
Lepidoptera		
Moth.....	Adult	Yes
Measuring Worm.....	Larva	Yes
Caterpillar.....	Larva	Yes
Unidentified.....	Adult	Yes
Caterpillar.....	Larva	No
Monarch Butterfly.....	Adult	Yes
Diptera		
Crane Fly.....	Larva	Yes
Deer Fly.....	Adult	Yes
Tachina Fly.....	Adult	Yes
Hymenoptera		
Carpenter Ant.....	Adult	Yes
Honey Bee.....	Adult	Yes

The fruits of some other plants were also readily eaten but to a seemingly lesser degree than for those listed in the preceding paragraph. The degree of utilization was designated as moderate. In this group are included fruits of various types: dry indehiscent fruits of *Echinochloa crusgalli*, *Poa palustris*, *Carex vulpinoidea*, *Rumex mexicanus*, *Polygonum pennsylvanicum*, and *Rosa blanda*; and the more or less fleshy fruits of *Vitis vulpina*, *Cornus Baileyi*, and

Sambucus pubens. The degree of utilization of these plant products indicate that they constitute preferred or staple foods.

For a third group of plants the fruits were eaten but only slightly. Included are the dry indehiscent fruits of *Calamagrostis canadensis*, *Spartina pectinata*, *Scirpus validus* and *Carex scoparia*, and the more or less fleshy fruits of *Prunus pennsylvanica*. This group is definitely not included in the preferred list of foods but could possibly be classified as emergency foods.

The fruits of 15 plants, representing 11 families, were not eaten. These included: *Typha latifolia*, *Cyperus strigosus*, *Scirpus atrovirens*, *Salix* sp., *Corylus americana*, *Alnus incana*, *Chenopodium album*, *Trifolium hybridum*, *Rhus hirta*, *Cicuta maculata*, *Asclepias syriaca*, *Asclepias incarnata*, *Phlox pilosa*, *Plantago major* and *Rudbeckia hirta*.

These data indicate that, in general, the starchy fruits of the Gramineae and the more or less fleshy fruits of various groups of plants are more heavily utilized than are other plant materials. With certain exceptions, small, dry, and/or hard fruits were not readily eaten. Plant parts, other than fruits and seeds, constituted a very minor portion of the plant materials utilized. These assumptions are supported, in part, by the work of others. Concerning the food of *Z. h. campestris* Bailey (1926) states, "In the examination of a great many stomachs of these jumping mice, nothing has been found but the fine white pulp of carefully shelled, well-masticated seeds. Generally these are from grasses, although grain and a variety of other plant seeds are eaten." Sheldon (1934) reports that captive *Zapus* ate seeds of many kinds of grass and sedge, green cones of hoary alder, wintergreen berries, huckleberries, apple, cucumber, cabbage, and sunflower seeds. Hamilton (1935) gives examples as follows: "An adult male collected in a swamp at Freeville, New York, had been feeding extensively on blueberries. An individual collected at Mays Landing, New Jersey, on May 15, 1931 had what appeared to be black muck in the stomach, with a few minute black undetermined seeds. . . . In captivity the animals freely ate currants, blackberries, raspberries, the seeds of tomato, melon and sunflower seeds. . . ." Sheldon (1938) lists strawberries, blackberries, raspberries, red baneberries, and sunflower seeds as having been eaten by captive *Zapus*.

Twenty-eight species of insects, representing 10 orders, 2 Gastropods, 1 Arachnid, and 1 Diplopod were made available to the caged mice as summarized in Table 6. Except for carrion beetles (Silphidae), lady bug beetles (Coccinellidae), and one of the larval Lepidoptera (Papilionidae) all were wholly or partially eaten. Although certain parts of some insects were not utilized (wings of Lepidoptera, head capsule and elytra of some beetles, covering of prothorax in some instances, jumping legs of grasshoppers, other miscellaneous chitinous parts) it is difficult if not impossible to designate certain insects or groups of insects as being more palatable than the others of those utilized on the basis of these quali-

tative observations. A more quantitative study would doubtless reveal the fallacy of such an assumption. The observations indicate these rodents are highly insectivorous and suggest they consume many insects under natural conditions. This assumption is supported by the reports of others. Schmidt (1931) reported that 2 specimens of *Z. hudsonius* had eaten several yellow geometrid caterpillars that feed on the sweet fern. Sheldon (1934) found the remains of insects in a few stomachs. Hamilton (1935) also found traces of insect remains in the stomachs of dissected specimens and further reports that captives freely ate small cutworms while one consumed a slug.

HOME RANGE STUDIES

Home range studies by trapping were made in 1941 at Itasca Park, Clearwater Co., Minn., between July 29 and Aug. 26. Thirty-eight *Z. h. hudsonius* were live-trapped, marked, released, and retrapped on an area of approximately 2.86 acres. More intensive investigations were made in 1947 between May 20 and Oct. 11 at Centerville, Anoka Co., Minn. Eighty-one *Z. h. campestris* were live-trapped and marked on 3 areas totaling approximately 37.07 acres (2.12, 9.67, 25.25 acres). Five others found in a nest were marked and released. Several adjacent areas were snap-trapped simultaneously with the live-trapping operations.

Swinging door type tin and wooden traps were used (Fig. 11). The traps were arranged in a grid pattern as described by Burt (1940) and Blair (1940). At Itasca the distance between traps was 30 feet (paced) and the traps were allowed to remain in place and continuously baited. At Centerville the distance was increased to 60 feet (measured). The areas were laid off in 60 foot squares with a tape measure and a numbered, wooden stake was driven at each corner marking the location of stations. The stations were not trapped continuously. Alternate rows were trapped each week to reduce the influence that the traps might have on the normal activity of the animals. The traps were placed differently at Itasca and Centerville because of the difference between the respective communities, Itasca being the richer area. Blair (1941) suggests that the distance between traps should be governed by local conditions.

When caught the first time, the mice were marked for future identification by clipping a digit or digits according to a prearranged code. Since 86 was the greatest number marked in one locality it was not necessary to clip more than 2 digits from any individual.

METHOD OF COMPUTING HOME RANGES

Several variations have been used for estimating home ranges from live-trapping data. The chief difference is in the amount of territory allotted to the known part of the home range as determined by the trapping records. The extremes are represented by the minimum method of Dalke & Sime (1938) and Lay (1942) and the quadrat method of Blair (1940).

Variations of the quadrat method have been used by Burt (1940), Haugen (1942), and others. Mohr (1947) reviews the various methods.

Blair (1940) in estimating home ranges, drew the study plot to scale on cross ruled paper. Each square represented 225 square feet in his work with the meadow mouse and his calculations proceeded as follows: "If an animal was always caught in only one trap, it would be statistically correct to consider that on the average the home range of that individual would extend half the distance to the nearest traps in which it was not taken. Thus, with the traps set 60 feet apart in lines separated by the same distance, the home range . . . would contain 16 squares or 3,600 square feet. If the vole were caught in two adjoining traps in a line its home range would include 32 square or 7,200 square feet. If an animal were captured in two traps in the same line separated by traps in which it was not taken, one unit of 16 squares would be allowed for each of the traps in which it was caught and one for every intervening trap. In many cases the home ranges extended diagonally across trap lines so that no such simple figure was formed. In these instances a 16-square rectangle (12 where the lines were only 45 feet apart) was drawn around each most distant trap. Then the outer corners of these rectangles were connected by straight lines and the squares within the irregular geometric figures thus formed were counted to determine the area of the home range. Squares that were only partially contained were counted as one-half."

Except for the elimination of known blanks, Blair's method is followed in the present study. Several of the calculated home ranges at Centerville would include parts of a cornfield if computed solely by this method. Trapping in these cornfields (1090 trap nights) indicated that jumping mice avoided them for the most part. Only 1 was caught within and it had penetrated only 10 feet. Except for a 10 foot strip inside the margin, all parts of cornfields were eliminated in calculating individual home ranges.

Those caught less than 4 times were eliminated from home range calculations chiefly because an examination of all data indicated that, in general, those caught less did not provide an adequate trapping record. Those having home ranges extending to traps on the periphery of the study area are eliminated providing the habitat was suitable for jumping mice beyond the peripheral traps in which they were taken. No attempt is made to group the home ranges by periods, as in some previous studies. The reasons are discussed later.

SIZE OF HOME RANGE

Five males and 4 females at Itasca provide sufficient data for computations. The size of the individual female home range ranged from .19 to .87 acres with a mean of .38 acres. The size of the individual male home range ranged from .14 to 1.10 acres with a mean of .43 acres. These data suggest that males have a larger home range than females

but too few data are available for conclusions.

Data are sufficient for the computation of 9 male and 17 female home ranges at Centerville. The sizes and shapes of representative individual home ranges are shown in Fig. 14. The mean home range for males was $2.70 \pm .50$ acres while the mean home range for females was $1.57 \pm .22$ acres. The difference between these two means is 2.07 times the standard error of their difference which is significant at the 5 per cent level.

Seton (1909) believed jumping mice travel farther than any of the other mice. Townsend (1935) concluded that jumping mice are of wandering habits correlated perhaps with a tendency to concentrate its population as the habitats became dry during the summer. Sheldon (1938) marked and released several jumping mice but secured too few data for definite home range calculations. She concluded they wander around considerably from month to month. Blair (1940a) secured home range data for *Z. h. hudsonius*. The mean home range of 26 monthly home ranges of males was $.89 \pm .11$ acres. Twenty-four monthly home ranges of females averaged $.92 \pm .11$ acres.

The home ranges reported by Blair are larger than those at Itasca. Although Blair's data are based on more than 5 times as many individual home ranges as the Itasca data, the number of catches per individual is about the same. The Itasca home ranges are based on an average of 4 catches per individual for both males and females while Blair's data are based on an average of 4.9 catches per males and 4.4 catches per females. The Centerville home ranges are much larger than those reported by Blair. Although the average number of catches per individual is greater (males 6.2, females 7.4) it hardly seems possible that this could account for the discrepancy in size of mean home range. A possible explanation is offered in the following section.

RELATION BETWEEN THE SIZE OF THE HOME RANGE AND THE ENVIRONMENT

Two types of data, ranges of individuals which have shifted and the ranges of animals under two different ecological conditions, i.e., Itasca and Centerville areas, give a degree of comparison of relative home range size in different habitats.

The record of No. 2, adult male, Centerville supplies information on home range size for the same individual in different but closely related habitats of the same general area. This mouse was caught 10 times on Plot 1 over a period of 29 days and utilized an area of approximately 4.37 acres. He moved to Plot 2 and was caught 7 times in 14 days. The size of the calculated home range was 2.20 acres, approximately $\frac{1}{2}$ as large as the home range for Plot 1. Although the number of catches, as well as the number of days over which the catches extended, is greater for Plot 1, these data seem comparable since neither of these factors significantly influenced the size of the home range for the Centerville data (discussed later). An examination of the areas covered on the 2 plots reveals one obvious difference, density

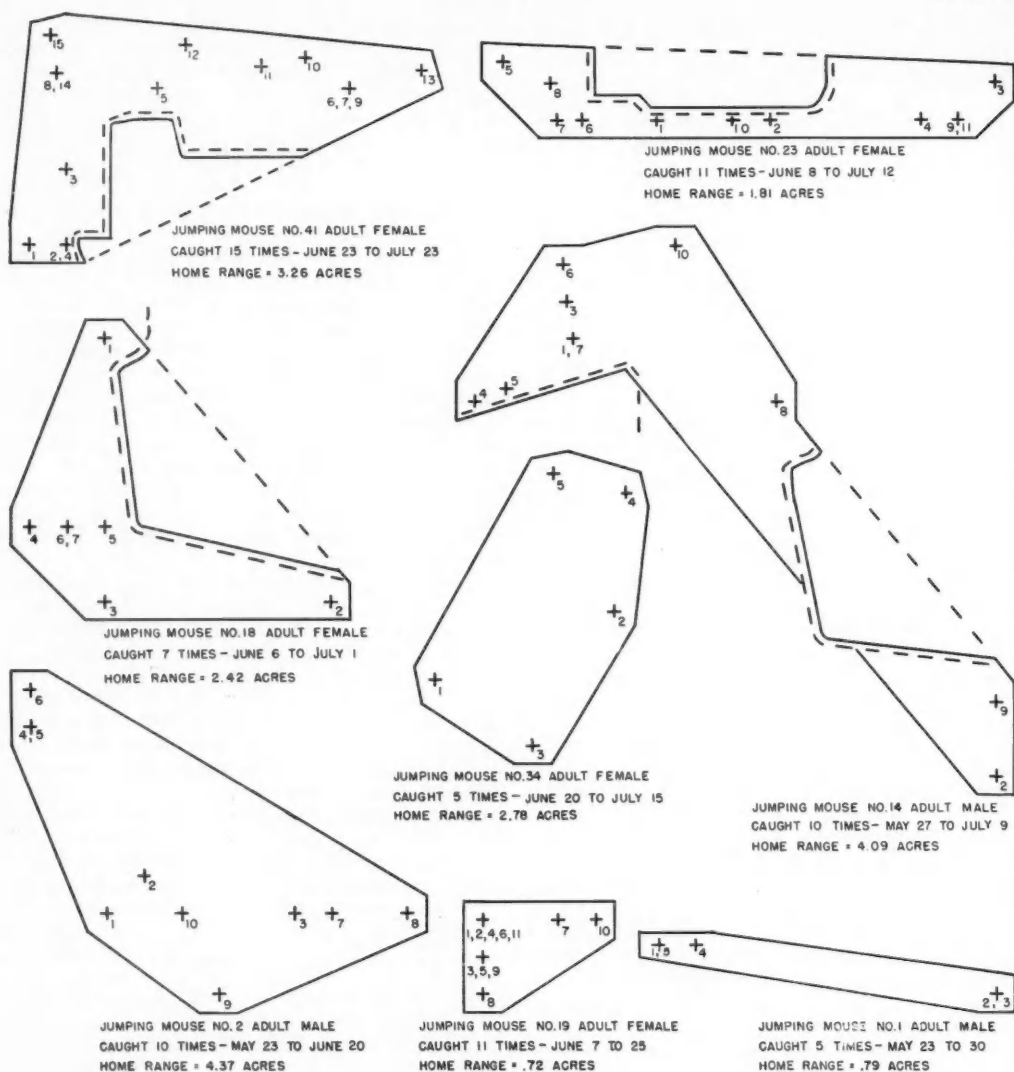


FIG 14. Outlines of individual jumping mouse home ranges as determined by trapping, Centerville, Minn., 1947.

+ Designate trap positions where jumping mouse was caught; 1-15 numbers indicate the position of each individual catch; — limits home range; --- boundary of cultivated field falling within home range figure as determined by connecting the outermost traps where animal was caught, excluded from home range except as indicated.

of cover. About $\frac{1}{3}$ of the home range on Plot 1 was a grazed pasture. The remainder, except a few spots, did not support the luxuriant vegetation found on the area covered by the home range on Plot 2. It seems possible that this difference in ground cover could account for the difference in home range size for the 2 plots.

The mean home range for Centerville is much larger than for Itasca. Calculating both sexes together the mean home range for Itasca was $.41 \pm .11$ acres while the mean home range for Centerville was

$1.96 \pm .24$ acres. The difference between these two means is 5.75 times the standard error of their difference, which exceeds the 1 per cent level of significance. These data indicate that the size of the home range of *Zapus hudsonius* is greatly influenced by the immediate surroundings. The data of Blair (1940a) likewise support this conclusion.

Although the size of the home range is doubtless characteristic of a species it surely varies within certain limits and the influence of the environment on this variation may be of great importance. It is

probable that the home range of an animal is variable, changing with environmental conditions. The changes resulting from seasonal aspects, disturbances, physiographic factors, and natural succession would seemingly have an effect on the activity of the animals present including the shape, size, and location of the home range. In case of the jumping mouse, the lowering of the water table has been observed to change the per cent of habitable range in a given area (see populations).

The area at Itasca was much richer than the Centerville area and supported a larger per acre population of jumping mice (see populations). The greater density at Itasca could possibly account for the smaller home range of individuals. This possibility has been suggested by Burt (1943). He said, "Population density also may influence the size of the home range and cause it to coincide more closely with the size of the territory." Or the smaller mean home range for Itasca might be due to the community structure. Perhaps the necessities of life were in closer proximity or juxtaposition at Itasca than at Centerville.

It is possible that some of the difference in the calculated mean home range size for Itasca and Centerville was due to the spacing of the traps. The interval was twice as great for Centerville as for Itasca. This possibility is suggested by Mohr (1947) who is of the opinion that the "Use of quadrats gives results varying directly with the size of the quadrat, the larger the quadrat in relation to the size of the real home range, the larger the area." The results indicate, however, that the spacing was approximately correct for each of the areas or, at least, that the ratio of spacing was approximately correct when comparing one area with the other. It seems improbable that the difference in spacing could account for more than a small portion of the difference between the size of the calculated mean home range for the 2 areas.

The jumping mouse at Centerville, *Z. h. campestris*, is subspecifically distinct from that at Itasca, *Z. h. hudsonius*, but it hardly seems possible that the slightly larger body proportions of the former could account for such a large difference in home range size.

The data are meager and not wholly comparable but suggest that the environment plays a major role in determining the size of the home range. Certain other workers have submitted data in support. These include: Blair (1940) reported that male meadow mice had smaller home ranges in moist than in dry grassland. Linduska (1942) found that prairie deer-mice and meadow mice with winter quarters in shocked corn did not range as widely as those living in adjoining fields of wheat stubble and meadows. Stickel (1948) reports that *Peromyscus leucopus* living in the uplands ranged more widely than those living in the bottomlands on her study plots in Maryland.

CORRELATION OF HOME RANGE SIZE WITH NUMBER OF CATCHES

In estimating home range size from trapping data one is confronted with deciding how many catches are necessary before the approximate size is indicated. It seems obvious that no set rule can be established since the efficiency of trapping and other conditions doubtless vary in different situations. The size of the home range is influenced by the environment. Except for relatively stable habitats, it would be difficult to determine the opportune time for calculating since the size of the individual home range may be changing in response to environmental conditions. Haugen (1942) and Blair (1942) attempted to solve this problem. Blair in calculating home ranges of woodland deer-mice excluded all individuals caught less than 10 times because, "those that were caught many more times than that seldom ceased to increase the size of their known home ranges until the tenth or later capture." Haugen, working with the cotton tail, continued until additional catches did not increase the size of the known home range before including an individual in his calculations.

In analyzing the 26 home ranges at Centerville it was not feasible to use such a system. In some instances such a method seems to have merit. No. 18, adult female, for example, was caught 7 times. The first 4 catches increased the known size of the home range while the last 3 did not. It is possible that an additional catch would have increased the known size of the home range. This point is illustrated by No. 41, adult female, caught 15 times. Catches 1, 2, 3, 5, 6, 8, 10, 12, 13, and 15 increased the size of the known home range while catches 4, 7, 9, 11 and 14 did not. The location of each catch is numbered in the diagrammed home ranges (Fig. 14). A check of these shows the impracticability of attempting a system such as those of Blair and Haugen in the present study.

The number of catches varied from 4 to 10 for the males and from 4 to 15 for the females on those figured in the home range calculations for Centerville. It would seem probable that the number of catches would have a significant influence on the size of the calculated home range. Both males and females show a positive correlation between the number of catches and size of home range (males .54, females .26) but in neither case is the correlation significant. The female having the largest home range (No. 32, 3.38 acres) was caught only 6 times while the female having the smallest home range (No. 68, .56 acres) was caught 7 times. The male having the largest home range (No. 39, 4.40 acres) as well as the male having the smallest home range (No. 11, .25 acres) were each caught 4 times.

These data are interpreted as indicating that the inclusion of those caught as few as 4 times in calculating the mean home range is justified and that the spacing and rotation of the traps was satisfac-

tory since only a few captures were necessary before the approximate size of the home range was indicated. As has been pointed out by others, it seems desirable to catch the animals as few times as practicable to eliminate, so far as possible, the influence of trapping on normal behavior.

CORRELATION OF HOME RANGE SIZE WITH PERIOD OF TIME OVER WHICH CATCHES EXTENDED

For the Centerville data, the period over which the catches extended varied from 5 to 40 days for the 9 males and from 9 to 41 days for the 17 females. The time element did not have a significant effect on the home range size. For both males and females there is a positive correlation (males .60, females .43) but in neither case is it significant. The largest female home range (No. 32, 3.38 acres) extended over a period of only 25 days whereas No. 24 had a home range of only 1.04 acres extending over a period of 41 days. For the males, the largest home range (No. 39, 4.40 acres) covered a period of only 22 days while No. 29 had a smaller home range 3.05 acres extending over 40 days.

SHAPE OF THE HOME RANGES

An examination of the diagrammed home ranges (Fig. 14) reveals a marked difference in their relative shapes. In general, the shape of the home range was determined largely by terrain features, cover, and land use of the immediate area. No. 23, adult female, Centerville, for example, exhibits a long and narrow home range. Her movements were closely associated with the small stream that flows through the area thus accounting for the long and narrow home range. No. 34, adult female, exhibits a more rounded and compact home range associated with the rounded swamp in which she lived.

SHIFTING HOME RANGES

One of the most perplexing problems was that most jumping mice suddenly disappeared from the catch. Three explanations seem plausible: the animal was a victim of predation, moved, or became "trap wise." The first 2 seem more logical. Although no specific instances of predation were observed, there is evidence of individuals permanently moving from one area to another. Three were known to have moved distances of approximately $\frac{1}{2}$ mile. No. 2, adult male, Centerville, was caught 10 times over a period of 29 days on Plot 1. He disappeared. Eight days later he was caught on Plot 2, a distance of about $\frac{1}{2}$ mile from the point where he was last taken. This mouse apparently established a "new home" on Plot 2 for he was taken 7 times over a period of 14 days. He again disappeared, perhaps to establish somewhere else. No. 9, adult female, Centerville was caught on Plot 1 May 26 and was not seen again until Sept. 15 when trapped on Plot 2. This represents a movement of about $\frac{1}{2}$ mile (straight line) in 3 months and 11 days. No. 15, adult male, Centerville was caught only twice, June 4 on Plot 1 and July 18 on Plot 2. He moved at least $\frac{1}{2}$ mile in 1 month and 14 days.

The data indicate that these mice commonly do not spend their entire lives in one locality as reported for deer-mice by Burt (1940). The record of No. 2 presents a clear-cut case of emigration of an adult over a distance of at least $\frac{1}{2}$ mile. Nos. 9 and 15 present definite evidence of emigration or nomadism. The fact that all individuals eventually disappeared from the catch is suggestive of emigration or nomadism. It seems that the home ranges of these mice are relatively unstable shifting from place to place in response to unknown conditions. Townsend (1935) and Sheldon (1938) suggest they are of wandering habits. Additional data are given under homing and populations.

In all 3 cases the movements were between Plots 1 and 2, the extremes of which are separated by more than $\frac{1}{2}$ mile, whereas no movements were known to occur between Plots 2 and 3 separated only by a gravel road. No marked mice were caught on any of the snap-trapping areas all of which occurred on the opposite side of this road in respect to Plots 1 and 2. The writer feels that this is especially significant since Plots 2 and 3, except for the intervening road, were continuous along a small stream which provided excellent habitat. Plots 1 and 2 were separated by a broad expanse of cultivated fields and heavily grazed pastures which constitute very poor habitat for this species. There was a travel lane of continuous heavy cover along fence rows and low swampy areas connecting the western extremes of the plots. All trapping records for Plots 1 and 2 indicate that the 3 utilized this travel lane in negotiating the distance between the plots.

These data seem even more significant in view of the fact that, on the basis of numbers, the probability for movement between Plots 2 and 3 was about as great as for movements between Plots 1 and 2. Twenty-four, 59 (including 3 emigrants and 1 exotic), and 7 marked jumping mice were known to occur at one time or another during the course of the summer on Plots 1, 2, and 3 respectively.

All evidence indicates that they move only under the protection of heavy cover. None were known to cross cultivated fields or heavily grazed pastures. More striking is the fact that none were known to cross a road separating two excellent habitats. Davis *et al* (1948) give similar data for the brown rat. Their studies indicate that these rodents seldom cross streets.

HOMING INSTINCTS

Thirteen jumping mice were released at points varying from .2 to .5 miles from the point of capture.

Two returned to their home areas. One apparently did not become "oriented" at once for she deviated about 200 yards to the left of a straight course for "home" where she entered a trap. She was released at this spot and was found in a trap 60 feet further removed the following morning. Following release at this spot, she was not seen again for 6 days when found in a trap 120 feet from the point originally taken. She was caught 2 additional times in this immediate vicinity. The other apparently started

for "home" soon after release for she was found in a trap between the point of release and her home site the following morning. She was caught twice more in traps between the point of release and her home site. After a period of 17 days she was caught in her original home range.

One was caught about 150 yards from her former home site about 1 year after release. This can in no manner be considered a return home as it seems almost certain she could not have avoided the numerous traps set in this area during the 3 months following her release. The evidence suggests that she returned to the vicinity of her former home range by chance.

Two were trapped approximately 75 yards from the point released. The data suggest that one established in this new area, at least for a time, for she was caught twice in the immediate vicinity 13 and 15 days following release. The data are even less complete for the other since he was caught only once, in a snap-trap, about 1½ months after release. It seems possible that both had become temporarily established in this area.

No data are available concerning the fate of the remaining 8. It is almost certain that they did not return to their former home sites for it seems impossible that they could avoid the numerous traps set in these areas.

These data, although meager, suggest that jumping mice possess no such homing instinct as indicated for the deer-mouse by Johnson (1926), Murie & Murie (1931 & 1932), Townsend (1935), Hamilton (1937), and Burt (1940). It is true that 2 found their way home, but in the light of the behavior of all it seems logical to assume that chance wandering, rather than a homing instinct, brought them back to the areas they formerly occupied.

These data are further interpreted as adding support to the conclusion that the home range of the jumping mouse is relatively unstable, for it seems that the number of returns would have been greater had the "home ties" been greatly developed.

POPULATION STUDIES

In light of the works of Burt (1940), Blair (1940, 1940a, 1940b, 1940c), and Stickel (1946) it seems that the proper use of live-traps yield reliable population figures for small mammals. Population figures per unit area for jumping mice are available from the trapping data at Itasca Park in 1941 and for Plot No. 2 at Centerville in 1947.

The method of analysis of data is basically the same as that of Burt, Blair, and Stickel. The calculations proceeded as follows: Only those areas that were more or less complete units were considered adequate. The results were broken down into monthly periods and all animals known to occur on the area were considered as comprising the population. Only live-trapping data were considered except for Sept. on Plot No. 2 Centerville where snap-trapping data were used. This seemed justifiable since this plot was somewhat isolated and had been live-trapped during the 3½ months immediately preceding. The size of the area to be used in calculations

was determined by computing the area contained in the total home range figure of all mice on the plot. The area enclosed by this total home range figure was used directly unless the individual home ranges of some included peripheral traps at points where the habitat was continuous beyond. In this case, the populations of males and females were calculated separately and a strip equal to ½ the average of the greatest diameters of the home ranges was added at these points to allow for marginal animals. Burt (1940) and Blair (1941) suggest the addition of such a strip.

POPULATION DENSITIES

Forty-two jumping mice (including 4 unmarked animals that died in traps) were caught on the 2.86 acre study plot at Itasca Park. The trapping records indicated that the entire plot was inhabited. The east and west sides were bounded by black spruce, *Picea mariana*, and balsam, *Abies balsamea*, forest which constituted very poor habitat. At the north and south ends, the vegetative type was more or less continuous along the small creek flowing through the area making it necessary to add additional territory at each of these points for calculation purposes. These additions increased the size of the area to 3.39 and 3.72 acres for the males and females respectively. Eighteen females and 24 males gave population densities per acre of 4.83 females and 7.08 males or a total of 11.91.

Population figures are available for June, July, Aug., and Sept. 1947 for Plot No. 2, Centerville. In June, 17 females and 7 males were caught on 7.46 acres. At one point it was necessary to add additional territory, increasing the area for calculations to 8.53 and 8.78 acres for the females and males respectively. The population densities were 1.99 females and .79 males or a total of 2.78 per acre. For July, 11 males and 25 females caught on 10.08 acres gave per acre populations of 1.09 males and 2.48 females or a total of 3.57. It was not necessary to increase the size of the area for calculations. During Aug., 3 males and 7 females caught on 3.22 acres gave densities of .93 males and 2.17 females or a total of 3.10 per acre. In Sept., 36 on 19.83 acres gave densities of .75 males, 1.06 females and a total of 1.81 per acre.

Blair (1940a) gives population figures for the jumping mouse in Mich. His per acre figures were .2 for late May, 2.8 for early June, 5 for late June, 3.4 for early July, 4.3 for late July, 4 for early Aug., 2.2 for late Aug., 1.4 for early Sept., and 2.6 for late Sept. By averaging his early and late periods for each month, figures comparable with those in this study are obtained. The figures of Blair, based on monthly periods, are surprisingly similar (Table 7) to those obtained at Centerville.

TABLE 7. Comparison of Monthly Per Acre Densities of Jumping Mice in Mich. and Minn.

	June	July	Aug.	Sept.
Blair's Data (adjusted for comparison)	3.90	3.85	3.10	2.00
Centerville Data	2.78	3.57	3.10	1.81

By contrast the per acre population of 11.91 jumping mice for Aug. at Itasca is more than 3 times as great as the Centerville or Mich. data for the same month. This large discrepancy could possibly be due to the widely differing habitats although it is possible that the traps at Itasca were sampling a larger area than was suspected. This latter possibility seems improbable since all evidence, including the size of the mean home range, indicate a much higher density for Itasca than Centerville.

Townsend (1935) published population figures for the jumping mouse in New York. His figures ranged as high as 72 per acre and are probably too high since he used snap-traps in a "moving quadrat" which was not restricted to an isolated area. In any event his technique differs so widely from that used in the present study that the data hardly seem comparable.

RELATION BETWEEN TOTAL POPULATION NUMBERS AND THE AMOUNT OF HABITABLE AREA

Since jumping mice characteristically inhabit moist habitats, the water level of the small stream and numerous marshy areas on Plot 2 Centerville limited, during the greater part of the trapping period, the amount of territory inhabited and the size of the trapping area. Both changed from time to time. During the greater part of June the low marshy areas and the small stream were filled with water permitting the trapping of only 12.97 acres in their immediate vicinity. Trapping results indicated that only 7.46 acres of this area were inhabited. During July as the water table gradually lowered both the size of the trapping area and the amount of habitable area increased because much of the favorable habitat that had been covered was now exposed. The trapping area was increased to 24.13 acres but part of this was due to the inclusion of more of the upland area. The size of the inhabited area increased to 10.08 acres. All was due to the lowering of the water table. The lowering of the water table increased the amount of habitable area up to a certain point but over and beyond this it had the opposite effect. This was due to the drying out of moist habitat suitable for jumping mice. During Aug. the trapping area was increased to 25.25 acres, all due to the lowering of the water table, but the trapping record indicated that jumping mice had completely deserted the now dry marshes and were restricted to a narrow zone along the small stream comprising 3.22 acres. Although the stream bed became completely devoid of standing water it remained damp in spots during the entire period. For Sept., the conditions changed completely since jumping mice were widely distributed over the area even in the more mesic uplands. The trapping area was decreased to 24 acres due to farming operations but 19.83 acres were inhabited.

The most striking fact associated with the increase and decrease of habitable territory concerns the total population for the plot and the per acre density for the habitable areas. During June, 24 jumping mice were found on the area representing a per acre

density of 2.78. For July, both the total number and per acre density increased (36 and 3.57 respectively). During Aug., only 10 mice were caught but the inhabited area had shrunk to such an extent that this still represented a per acre density of 3.10 which does not differ greatly from the figures for June and July. For Sept. the total number of mice mounted to 36 but the habitable area increased to such an extent that this represented a population density of only 1.81 per acre.

The increase in total numbers as well as in density per acre for July seemed to reflect the addition of young of the year to the population since this age class was quite prominent in the catch. The figures for Aug. represent an unexpected drop in total population for the plot but plausible explanations seem available. The per acre density did not decrease markedly while both the total population and amount of habitable area shrunk considerably. This is suggestive of a saturation point associated with territoriality or a lowered security threshold associated with the amount of escape cover. If these animals exhibit a high degree of territoriality (which hasn't been demonstrated), it is entirely possible that competition for space in the shrinking habitat caused the emigration of much of the population. It is also possible that the decrease in total numbers could be the result of increased predation made possible by lowering of the security threshold for the plot as a whole. Either or both of these explanations seem reasonable on the basis of the data available for June, July, and Aug. since the per acre density for the 3 months did not vary greatly. The figures for Sept. offer a clue as to what may have happened during the previous month for the total population on the plot again increased. Although a portion of this increase could be attributed to reproduction the evidence indicates that some moved in from elsewhere. No. 9 was known to have moved from Plot 1. Nos. 45 and 65 give even more concrete evidence of movement away from and back to the plot for both were present in July and Sept. but absent in Aug. Despite the fact that the total number on the plot in Sept. more than tripled when compared with Aug., the density actually decreased due to much more of the area being inhabited. These data suggest that the density of jumping mice per unit of habitable area does not exceed a certain figure (4 per acre at Centerville) and that they do not concentrate in favorable areas as suggested by Townsend (1935).

STABILITY OF POPULATION

The population on Plot 2 was far from stable. Of the 90 known to occur naturally on the plot during the period May through Sept., 70 (77%) were found during only 1 month, 18 (20%) were found for 2 months, and only 2 (2%) were found for 3 months. The releasing of several at distances varying from .2 to .4 miles from their point of capture is doubtless responsible for the disappearance of 7 but even in the majority of cases where no interference occurred they disappeared.

Seven were marked on the plot in May, 6 disappeared before June 1 and 1 remained on the plot during June and July.

During June only 1 marked during the preceding month was caught. Twenty-three additional ones were marked and 10 of these disappeared by the end of the month. Twelve remained on the plot during July after which they disappeared and 1 remained through July, disappeared during Aug., and returned in Sept.

During July, 14 previously marked mice occurred on the plot. Thirteen had been marked the previous month while the remaining 1 was marked in May. Twenty-two additional mice were marked. During the month the following mice disappeared; the 1 marked in May, 12 of those marked in June, and 17 of those marked in July. The remaining mouse marked in June was absent in Aug. but reappeared in Sept. Four of the remaining mice marked in July were present during Aug. only and the other one was absent in Aug. but present in Sept.

For Aug., 9 mice occurred naturally on the area (not including No. 25 released there). Four had been marked during the previous month, while the remaining 5 were unmarked. All of the previously marked mice disappeared by the end of the month but one of the remaining ones was present in Sept.

During Sept., when the area was heavily snap-trapped, 36 were caught. Only 3 had been previously marked on the area, 1 in Aug., 1 in July and 1 in June. Neither of the mice marked previous to Aug. had been caught on the plot in Aug. Number 9, represented in the catch, was an immigrant from Plot 1.

Some possible causes for this rapid turn-over were discussed in the preceding section. Another is intimated in the following section.

POPULATION STRUCTURE

Three age classes were recognized among the individuals trapped on Plot 2; adults, subadults (with adult pelage but of small size), and juveniles (very small size and juvenile pelage). No young of the year appeared in the catch until July when 25% were either juveniles or subadults (3 juveniles, 6 subadults, 27 adults). Fifty per cent of those caught in Aug. were young of the year (5 subadults, 5 adults). The figures for Sept. are more difficult to break down into age classes since the young from early litters have all the appearances of adults at this time (see development of young). Sixty-one per cent (22) were doubtless young of the year and 8% (3) were definitely adults. The remaining 30% (11) appeared to be adults and were classified as such but in all probability some or all were young of the year. These data indicate that the over-wintering adults are, for the most part, gradually replaced by the young of the year as the summer progresses. The factors responsible were not determined but doubtless include death from predation, old age, and other natural causes.

SUMMARY

1. Certain aspects of the life history and ecology of the jumping mouse, *Zapus hudsonius*, were studied at various times during 1941, 1942, 1946, 1947, and 1948. The investigations were mostly in Minnesota but a few data were gathered in Wisconsin. Some individuals were live-trapped, marked, released, and re-trapped while others were caged and studied under laboratory conditions. Snap-trapped specimens were also examined.

2. Description, weights, standard measurements, and sex ratio are given.

3. The gestation period was determined by observing caged females; for non-lactating females, it was approximately 18 days.

4. The young were successfully raised in captivity. At birth they are helpless and devoid of hair. The eyes and ears are closed. Hair appears about the 9th day; the incisors erupt about the 13th day and the external auditory meatus opens about the 19th day. By the close of the third week, they are readily recognized as jumping mice. The eyes open between the 22nd and 25th days. Weaning is gradual and begins about the same time the eyes open. The juvenile pelage is replaced by the adult pelage during the 4th week.

5. Growth rates of the young are given. Most of the increase in body proportion occurs during the first 4 weeks. Except for the 2-week period following weaning, the rate of weight increase continues to be somewhat rapid at least through the 13th week.

6. Embryo counts and litters found in the field indicate that the average litter size is 5 or 6.

7. Data from the repeated examination of live-trapped females indicated that some adults had at least 2 litters during the summer. Circumstantial evidence indicated that some could possibly have had 3.

8. The examination of live-trapped and dead females indicated that female jumping mice of early litters breed during the first summer of their lives.

9. Data from the examination of live-trapped and dead females and an evaluation of the population structure on a study area throughout the summer of 1947, indicated that the dates June 15 to Aug. 30 approximately delimited the period during which parturition occurred. There were 3 peaks of births; 1 in the latter part of June, another in mid and late July, and a third in mid August.

10. Two examples of jumping mice that lived to be at least 2 years old, under natural conditions, are reported.

11. Habits such as locomotion, swimming, digging, defense mechanisms, activity patterns, voice, sociability, method of feeding, water consumption, cleanliness, and signs are described.

12. Evidence from macroscopic examinations indicated that the mice underwent a complete molt dur-

ing the latter part of August and early September, 1947. The molt progressed from front to rear and was generally completed in about 3 weeks.

13. Two cases of predation on jumping mice are reported. One involved a northern pike, *Esox lucius*, the other a weasel, *Mustela* sp.

14. Two species of fleas, *Megabothris quirini* and *Megabothris wagneri*, were commonly found as ectoparasites. Larval ticks, *Dermacentor variabilis*, and bot-fly larvae, *Cuterebra*, were also found but less commonly.

15. The habitat preference of the mice was determined by extensive trapping. Moist habitats such as that provided by grass and/or sedge meadows and willow-alder thickets, on the borders of streams or pot holes, were found to be favored.

16. Evidence is presented which indicates that availability of moisture is more important than vegetative type in determining whether jumping mice are present in a given area. Disregarding the water factor, there was evidence that certain vegetative types were preferred.

17. A more or less typical jumping mouse habitat is described.

18. Other mammals found associated with the jumping mouse are listed.

19. Nests found in the field and those constructed by captives are described. The nests occurred in a variety of situations such as hollow logs, underground, or on the surface but in general were somewhat similarly constructed from grass or leaves.

20. Dates of emergence from hibernation are given for 4 years. These dates are correlated with other phenological data. Evidence is given that the date of emergence can be predicted by observing the occurrence of certain phenological events.

21. Evidence is presented which indicates that obesity precedes the hibernating period. The fattest captives were the first to hibernate. All late field records were of mice in poor body condition or subadults.

22. A food preference study was conducted under laboratory conditions. Seeds of grasses, the fleshy fruits of various plants, and insects were, in general, heavily utilized.

23. Home range studies by trapping were conducted during 2 summers, each in different localities.

24. The size of the mean home range of the males, $2.70 \pm .50$ acres, was significantly larger than the mean home range of the females, $1.57 \pm .22$ acres, in the one area for which data were sufficient for comparison.

25. Two types of data were obtained which indicated that the size of the home range was influenced by the immediate surroundings. The first involved the same animal in 2 closely related habitats but differing in density of cover; in one the home range was 4.37 acres while in the other it was 2.20 acres. The second was the size of the mean home range in two widely separated areas of different types. The

size of the mean home range, $1.96 \pm .24$ acres, in one area was significantly larger than the mean home range, $.41 \pm .11$ acres, for the other.

26. Neither the number of times caught nor the number of days over which the catches extended significantly influenced the size of the home range.

27. The shape of the home range was largely determined by the general terrain features, cover, and land use of the immediate area.

28. Evidence is presented which indicates that the home range of the jumping mouse is relatively unstable.

29. The releasing of several mice at distances up to .5 miles from the point of capture did not indicate a marked homing instinct.

30. Population density figures based on trapping data are given for August (11.91 per acre) in one area and for June (2.78 per acre), July (3.57 per acre), Aug. (3.10 per acre), and Sept. (1.81 per acre) for another.

31. The data from population studies suggest that the mice do not concentrate in favorable areas.

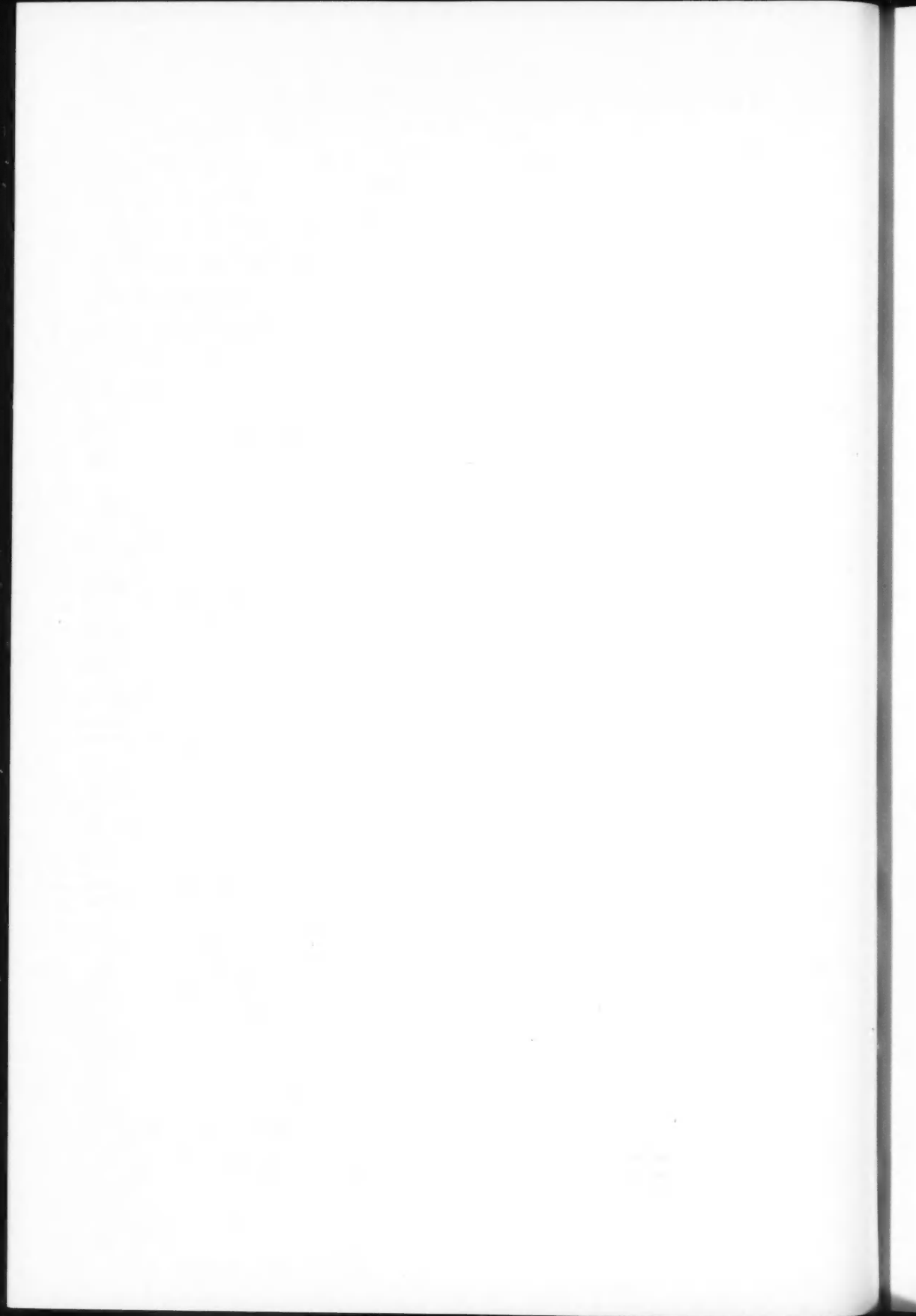
32. Evidence is presented which indicates that the population for a given area is rather unstable. Seventy-seven per cent of the animals were present in a study plot during only 1 month, 20% were resident during 2 months, while only 2% were resident during 3 months.

33. The overwintering population was gradually replaced by the young of the year during the summer of 1947 in a study plot.

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THE CENTIPEDES OF THE CHICAGO AREA WITH SPECIAL REFERENCE TO THEIR ECOLOGY

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INTRODUCTION

In the past, ecologic work on relatively unimportant economic groups has been done on single species, with the view of establishing their relations either to their own environment or to other individual species in a particular community. Only recently has work been started on the larger taxonomic categories with the view of working out the biology of a group.

The present study exemplifies many implied difficulties. Field work on organisms that can neither be identified at sight in the field, nor seen in the field without disturbing their ecologic relations, is productive of quantitative results only in an indirect way. It is not surprising then that the presentation of results obtained in such a manner often appears unspecific and certainly does not lend itself to as ideal a quantitative expression as does that of the standard laboratory approach. It was with these ideas and limitations in mind that the present study was projected.

The writer thanks Professor Orlando Park whose guidance, aid, and patience made this study possible. The writer gladly acknowledges his indebtedness to Dr. R. V. Chamberlin of the University of Utah for taxonomic assistance; to Messrs. Karl P. Schmidt, William J. Gerhard, and Rupert Wenzel of the Chicago Natural History Museum for the use of their facilities; to Dr. Eliot C. Williams, Jr. of Wabash College, Drs. Frank A. Brown, Jr., and Albert Wolfson of the Department of Biological Sciences, North-

western University, for their advice and valuable criticism during the course of this study.

GENERAL AREA OF STUDY

The Chicago Area already has an extensive botanical, geological, and zoological documentation. Pioneer botanical work in relation to local physiography was done by Cowles (1899, 1901). Shelford (1913a) made the first important study of the animals in the local biological communities. Park (1951) has summed up and brought to date all this documentation. Some general description is in order for the reader who is completely unacquainted with this area.

This region located about the southern tip of Lake Michigan is distinctive from several points of view. Geologically it is an area of comparatively recent glaciation, and, as such, encompasses a rather elaborate morainic area complete with several drainage systems, as well as part of the bottom of glacial Lake Chicago. Herein are striking changes in topography which manifest themselves in the varied vegetation found here. Another unusual feature of this area is the extensive sand dunes along the southern shores of Lake Michigan, wherein ecological succession is a visible fact.

With respect to the vegetation this area is the meeting place of several types of forests. These are the Beech-Maple, Hemlock-Hardwoods, Red Oak-Sugar Maple-Basswood, Oak-Hickory, Black Oak-

Hill's Oak, and Bur Oak forests. In addition to these latter the region at one time contained large tracts of prairie, and, a study of prairie centipedes also has been included. The localities, in which most of the collecting for this investigation was done, lie chiefly on the Lake Michigan side of the old Continental Divide, which in this region is represented by the unlands of the Valparaiso moraine.

West of Chicago beyond the lake plain are the morainic uplands alternating with lowland drainage valleys. These uplands present the most xeric of environmental conditions within the area. The Oak-Hickory forest is the climatic climax in the western part of the Chicago Area. On the highest and driest uplands the Black Oak-Hill's Oak or Bur Oak woodlands are found. These two forest types were probably physiographic climaxes on these uplands.

The valleys in this morainic area are occupied by streams in some cases. The flood plains of these streams are occupied by forests which reach an edaphic climax in the Red Oak-Sugar Maple-Basswood Association. This association is the physiographic climax in the ravines of the Lake Border moraines in the northern part of the area.

Since this morainic region is also along the prairie border, the forests literally interdigitate with the prairie here. Unfortunately except for a few scattered patches the prairie has long since disappeared. The forests too have suffered a great deal of disturbance but enough is left to reveal the essential character of the area.

The Beech-Maple Association is the climatic climax forest southeast of Lake Michigan and extending eastward through northern Indiana and southern Michigan. Within this area there are many forests that are not yet climax or that are so disturbed that it is impossible to determine their character in relation to the original primary successions.

The Hemlock-Hardwoods forests are along the east shore of Lake Michigan, beginning about at the Michigan-Indiana boundary on the sand dunes, and, extending northward and eventually eastward. These forests comprise an association that is climax only on sand dunes in this area.

Each of the natural areas mentioned are where they are because of a complex of historical, climatic, and physiographic factors. Studies of the physical environment of these areas have been made by Fuller (1914), Park (1931), Strohecker (1938), and others. Detailed descriptions of certain features of the vegetation of this region have been presented by Cowles (1899, 1901), Fuller (1925), Pepoon (1927), and Nichols (1935).

Within these major biotic communities there are many smaller communities each with its own microclimate. These in turn are subdivided into still smaller units, viz., the leaf mold and log societies. The log niches provided the greater part of the centipedes collected for this study.

LOCALITIES STUDIED IN THE CHICAGO AREA

The physiographic, edaphic, and human disturbances in the Chicago Area have resulted in forests

that today can be classified under one of three categories—wet, intermediate, and dry. This concept of wet, dry, or intermediate is based on the environmental conditions of the forest floor niches during the major part of the year. This classification is, in a sense, arbitrary for the purposes of this paper. It is not intended to substitute or conflict with the several accepted classifications of the vegetation of the area, but rather to serve as a working basis for the analysis of the rôle of certain environmental factors in the distribution of particular centipede species populations that are not distributed according to vegetation types but to environmental conditions under those types. For example, a forest with a thick, undisturbed canopy as can still be found in southern Michigan retains more moisture in the forest floor niches than an extensively cut forest of the same vegetational composition. Some description of each of them is necessary to demonstrate why they possibly fit under this artificial schema.

Indian Head Woods, Glenn, Michigan.—This forest is located about 1½ miles southwest of the small town of Glenn on the bluffs overlooking Lake Michigan. It is a Hemlock-Hardwoods community. The canopy trees are mainly sugar maple (*Acer saccharum* Marsh.) and beech (*Fagus grandifolia* Ehrh.). Hemlock (*Tsuga canadensis* Carr.) predominates on the upper terrace of an old floodplain that cuts through the forest. Other hardwood canopy trees found here include American elm (*Ulmus americana* L.), red oak (*Quercus borealis maxima* Ashe) and tulip (*Liriodendron tulipifera* L.). Although selective cutting has been going on for some years the bulk of the forest canopy is intact. The forest floor is covered with a very thick leaf mold, and old stumps and logs are present in large numbers. As a result of this heavy canopy and leaf mold insulation a wet environment is maintained on the forest floor. Since the area was a private game preserve for many years there has been little disturbance aside from the lumbering.

Dunes Forests, Saugatuck, Michigan.—This, like the previous forest, is a Hemlock-Hardwoods community. The canopy trees here are chiefly beech (*F. grandifolia*) and sugar maple (*A. saccharum*). Some hemlock (*T. canadensis*) is still found scattered here and there in the forest, but most of it has been cut. Disturbance is much greater here as a result of many trails having been put through the forest. Where the canopy trees have not been disturbed floor conditions are moist as a consequence of the thick leaf mold. Fewer logs are to be found here, probably a secondary effect resulting from the many summer cottages and lodges in the vicinity.

Warren's Woods, Lakeside, Michigan.—This is a Beech-Maple forest, probably the finest, because it has been least disturbed, in the Chicago Area. Its canopy of beech (*F. grandifolia*) and sugar maple (*A. saccharum*), along with American elm (*U. americana*), red oak (*Q. borealis maxima*), shagbark hickory (*Carya ovata* Koch.), basswood (*Tilia americana* L.), and tulip (*L. tulipifera*) is unbroken, except where the trees naturally have fallen. The forest floor has a large number of logs in all stages of

decay. The leaf mold is thick and wet. This forest contains the largest number of any of moist habitat niches for centipedes in this study.

Beech-Maple Forest, Ogden Dunes, Indiana.—This is another Beech-Sugar Maple forest, similar in composition to the preceding forest; but differing in that it occurs in small mesic "pockets" in the Dunes Park area. Within these pockets the trees form a dense canopy, which is usually surrounded on three or four sides by high sand dunes. As a result of this protection there is a thick layer of decaying leaves, logs and other organic matter on the underlying floor. This layer is damp, even during summer.

Davis Woods, Smith, Indiana.—This forest community contains representatives of at least three forest types. The major part of the forest is swampy and the forest floor is covered with standing water during a greater part of the year. The presence of water maintains this swamp forest as a physiographic climax. The canopy trees in this wet area are typical swamp forest species (*Acer rubrum* L., *U. americana*, *Ulmus fulva* Michx., *Quercus bicolor* Willd., *Fraxinus nigra* Marsh.). On the higher ground toward the periphery of the forest the canopy trees are sugar maple (*A. saccharum*) and beech (*F. grandifolia*). In portions where the beech and maple have been cut white oak (*Quercus alba* L.) and shagbark hickory (*C. ovata*) have grown up, indicative of the history of this vegetation. Forest floor conditions are relatively undisturbed. There is a wealth of decaying logs and stumps and the presence of water as mentioned, provides the most mesic of conditions.

Gloyeski Woods, Chesterton, Indiana.—This is a silt floodplain forest. It is constantly pastured and there has been some cutting. Most of the logs have been removed. The canopy trees include Sycamore (*Platanus occidentalis* L.), some sugar maple (*A. saccharum*), basswood (*T. americana*) and members of the red oak (*Q. borealis maxima*) and white oak (*Q. alba*, *Q. bicolor*) groups. The lower terraces are flooded every year and conditions are relatively moist. On the higher terraces where most of the cutting has occurred conditions on the forest floor become very dry during the summer.

Oak Woods, Glenn, Michigan.—These are groves of oak trees located on the bluffs above Lake Michigan one mile west of Glenn. Because of their location on the bluffs they are easily drained. In addition, the scantiness of the canopy allows the winds off the lake to blow away the leaf fall. Consequently the environment is very dry beneath these trees. Centipedes were taken from old stumps in the area.

Black Oak Forest, Dunes Park, Indiana.—This forest is a stage in the Dunes succession. This area suffers from disturbance and albeit there are leaf mold and logs present floor conditions are dry.

Black Oak Forest, Gary, Indiana.—This is a forest located on the sand ridges along the south shore of Lake Michigan. It probably is secondary as a result of burning. The undergrowth is still burned over periodically. Consequently there is no leaf mold on the forest floor and few, if any, logs. Here again

whatever centipedes found were taken in old cut stumps.

Oak-Hickory Woods, Palos Park, Illinois.—This forest community is composed chiefly of white oak (*Q. alba*), bur oak (*Quercus macrocarpa* Michx.), and shagbark hickory (*C. ovata*). It is located on the uplands which historically were occupied by the Oak-Hickory climax. Conditions within this forest are xeric. In this particular woods the large ant nests of *Formica ulkei* Emery are prominent.

Oak-Maple Forest, Tremont Dunes, Indiana.—This is predominantly a Black Oak-White Oak-Sugar Maple forest located on the sand dunes. Conditions within this forest are more mesic than in the previous forest. More leaf mold and logs are present. During the summer, however, conditions become xeric, only a few niches, such as the larger stumps, remain moist.

Deer Grove Park, Arlington, Illinois.—This is another upland forest located in the area where either Oak-Hickory or Bur Oak is climax. At present this forest is badly cut over and otherwise disturbed, so that its original character can only be conjectured. In the lowlands, sugar maple (*A. saccharum*) and basswood (*T. americana*) predominate; in the highest areas on the periphery bur oak (*Q. macrocarpa*) is found. White oak (*Q. alba*) and shagbark hickory (*C. ovata*) also make up a portion of the canopy. Many logs and a thin layer of leaf mold remain. In summer conditions within the forest become xeric.

Oak Woods, Ogden Dunes, Indiana.—This is another dunes sere forest very similar to the one at Tremont. However, in the locality studied only scattered patches are left. These have leaf mold on the floor, but most of the logs long since have been removed.

Carlé Woods, Desplaines, Illinois.—This is one of the floodplain forests so common along the Desplaines River in the western part of the Chicago Area. The predominant canopy trees here are red oak (*Q. borealis maxima*), sugar maple (*A. saccharum*), and basswood (*T. americana*). In the Chicago Area this a physiographic and edaphic climax. The forest rests on glacial outwash consisting mainly of gravel. The floor of this forest is usually flooded in the spring and for a time the thin layer of leaf mold as well as the logs and stumps are very moist. But with the onset of summer the forest dries out rapidly. On the whole environmental conditions within this forest are not as wet as those of the southern Michigan or northern Indiana forests (Warren's Woods, Davis Woods) nor as dry as the various oak forests.

Thatcher, Schiller, Pottowotamie Woods, Cook County, Illinois.—These forests are all located along the Desplaines River valley. The canopy trees composing them include basswood (*T. americana*), sugar maple (*A. saccharum*), red oak (*Q. borealis maxima*), swamp white oak (*Q. bicolor*), American elm (*U. americana*), white oak (*Q. alba*), and shagbark hickory (*C. ovata*). Intermediate moisture conditions prevail in these woods.

Peacock Prairie, Glenview, Illinois.—This is a ten

acre patch of prairie located near the junction of U. S. highways 21 and 58, about 8 miles west of Evanston, Illinois. It is just west of the Glenwood Beach of glacial Lake Chicago. It is the property of a private estate and as far as can be ascertained (Paintin, 1929) it has never been plowed, certainly not in the last fifty years. With respect to the vegetation it is an example of the low swamp prairie typical of the prairie border in this vicinity.

Private subdivision, Glenview, Illinois.—Low prairie similar to the one above, but in this case the area has been cut and burned over and probably also plowed sometime in the past.

Prairie, Palos Park, Illinois.—This is grassland that has been plowed and cultivated in the recent past. Vegetation is only vaguely reminiscent of the original prairie flora.

Centipedes were collected in the preceding localities representing the major biotic communities within the Chicago Area. From these data the distribution pattern was worked out. In the course of this work life history data were gathered whenever possible as well as any additional information having a bearing on the problem.

Quantitative Berlese samples were taken weekly over a period of a year from a section of prairie and from a Red Oak-Maple-Basswood forest. These were brought back to the laboratory and processed through Berlese funnels. It was hoped that some idea of the centipede population in these two communities could be obtained by this method.

Earlier work in Champaign County, Illinois, both in laboratory and field (Auerbach, 1949) had indicated a positive relationship with relative humidity. To substantiate this, additional humidity gradient experiments were carried on using the method of Lunn (1939). Carrying this idea still further, centipedes were brought into the laboratory where they were subjected to desiccation under constant humidity and constant temperature conditions. By this method it was hoped that some indication of the factors underlying their present distribution would be obtained.

DISTRIBUTION

Four of the five known orders of Chilopoda are found in the Chicago Area. These are grouped into 21 genera which include 30 species (Table 1). Verhoeff (1925) has classified the European chilopods into various ecological groups depending upon the particular niche which they occupy. Thus certain species were called log-inhabitants; others, under-rock inhabitants, river bank inhabitants, beech forest dwellers, etc. The present study of centipedes was started with this idea in mind. But as field work progressed the evidence accumulated that such a classification is too narrow for the centipedes in this area. On the contrary the majority of the species seem to be uniformly distributed within each of the local communities. Certain exceptions to this include the prairie species and centipedes in ant nests and niches associated with human activities, e.g., rock gardens and wood piles. Nevertheless cer-

tain differences in the density of species distribution became manifest. Certain species appeared to be more abundant in one type of forest than in another. The quantitative distribution data for the most common species collected have been grouped under the major communities listed (Fig. 1). The ethopolid, *Bothropolys multidentatus* (Newport) comprises the largest percentage of centipedes collected in the wet forest communities. The other common species of Lithobiomorpha in this size category, namely, *Lithobius forficatus* Linne and *Neolithobius voracior* (Chamberlin), are found sparingly; the bulk of those actually taken were found in the grazed portions of Gloyeski woods.

In the intermediate forest communities *N. voracior* represents about 55% of the common centipede population; *L. forficatus* represents 22%; and *B. multidentatus* 15%. In the dry forests, *N. voracior* and

TABLE 1. Check list of Chicago area chilopods.

** Not taken in the Area but reported from surrounding areas; * Reported from Area, but not taken by writer; † Personal communication of Mr. Henry Dybas, of the Chicago Natural History Museum.

Order Scutigermorpha

Scutigeridae

Scutigera forceps (Rafinesque)

Order Lithobiomorpha

Lithobiidae

Lithobius forficatus Linnaeus

Neolithobius voracior (Chamberlin)

Neolithobius tyrannus Bo'llman

Sonibius politus (McNeill)

Sonibius numius (Chamberlin)

***Sonibius bius* (Chamberlin) 1922

Nadabius iowensis (Meinert)

**Nadabius ameles* Chamberlin 1944

Pastobius sp.

Pokabius bilabiatus (Wood)

***Pokabius bilabiatus verdecens* Chamberlin 1922

***Tidabius tivius* (Chamberlin)

†*Tidabius suitus* Chamberlin

Tidabius anderis Chamberlin

**Sigibius urbanus* Chamberlin 1944

Henicopidae

***Lamyctes fulvicornis* Meinert

***Lamyctes pius* Chamberlin

Ethopolidae

Bothropolys multidentatus (Newport)

Order Scolopendromorpha

Cryptopidae

Cryptops hyalinus Say

***Theatops spinicaudus* (Wood) 1863

Otocryptops sexspinosus (Say)

Order Geophilomorpha

Soniphilidae

Soniphilus embius Chamberlin

Poaphilus kevinus Chamberlin

Linoteniididae

Linolenia chionophila (Wood)

Linolenia fulca (Sager)

Geophilidae

Pachymerium ferrugineum (C. L. Koch)

Arenophilus bipuncticeps (Wood)

Geophilus rubens Say

Schendylidae

**Schendyla nemorensis* (C. L. Koch) Chamberlin 1944

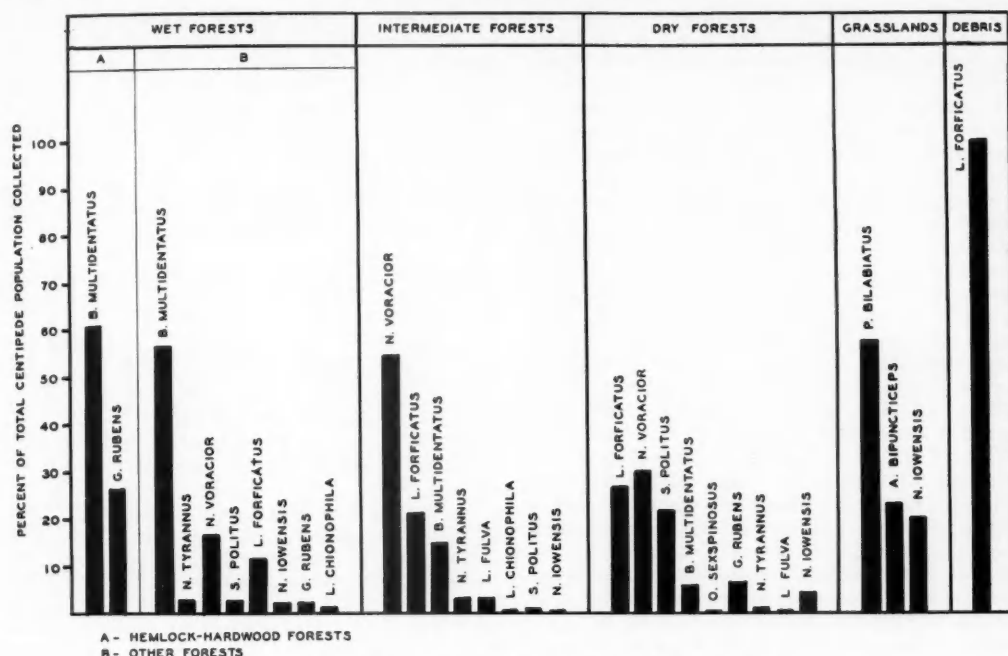


Fig. 1. Distribution of the common centipedes in the Chicago Area.

L. forficatus are present in almost equal numbers. The percentages are 30 and 27 respectively, while *B. multidentatus* represents only 6%.

Geophilus rubens Say, *Sonibius politus* (McNeill), and *Nadabius iowensis* Meinert, are also represented in varying numbers. However, their peculiarities of distribution are such, that to attempt to correlate them with regard to the three species mentioned first would at present, be going beyond what data are available.

It should be borne in mind that collections were not made on a strictly quantitative basis. This group of animals does not lend itself readily to a particular technique. To circumvent this situation, collecting was done in a uniform pattern in each of the forest communities. Logs were broken open, bark was stripped from dead standing trees and from logs, old stumps were broken up, and the leaf mold was sifted by hand. While these techniques are sufficient for securing the majority of the large centipedes, they are not adequate for all of the smaller species.

Only by the most careful of techniques, such as the Berlese funnel method, can these smaller centipedes be acquired in numbers. This is particularly true for those small lithobiids that spend most of their time on the forest floor, but not in logs. Still others, for example certain geophilids and certain scolopendrids, inhabit deep niches such as the center of logs, the roots of stumps, and the soil. In spite of the fact that these are shown on the checklist (Table 1) and are discussed at various lengths in the species discussions, not enough of them were taken to be used statistically or experimentally.

In the grassland area of this region three species appear to predominate. Two of these (*Nadabius iowensis* and *Arenophilus bipuncticeps*), from previous reports in the literature, seem to be ubiquitous throughout temperate North America. In the Chicago Area this continues to hold true for only one of them, viz., *N. iowensis*, which, as can be seen in the graph (Fig. 1), also is present in the forest. *Pokabius bilabiatus* (Wood) with 56% of the population forms the bulk of the prairie Chilopoda. *Arenophilus bipuncticeps* (Wood), with 23% of the population, is the next largest group.

In the niches associated with human activities the predominant species seems to be *Lithobius forficatus*. Further collecting may demonstrate otherwise, but to date, this species was the only one collected.

The nests of two species of ants have yielded various species of centipedes. Holmquist (1926) in a study of the nest of the mound-building ants *Formica ulkei* E., listed the following species of centipedes: *Pokabius bilabiatus*, *Nadabius iowensis*, *Pachymerium ferrugineum*, *Soniphilius embius*, and *Arenophilus bipuncticeps*. Of these the writer has taken *N. iowensis* and *P. ferrugineum*. In addition he has collected young specimens of *Otocryptops sexspinosus*. *P. ferrugineum* and *S. embius* were taken in the nests of *Lasius umbratus mixtus aphidicola* by the writer.

GENERAL BIOLOGY

Scutigera forceps (Rafinesque)

This is one of the commonest species of centipedes. It is known as the "house centipede." As its com-

mon name indicates it frequently is an inhabitant of man's abodes. It reaches a maximum size of 27 mm., but its long, almost feathery legs give it an appearance of much greater length. This genus, morphologically and probably physiologically, is the most specialized of the Chilopoda. Their seven dorsal stigmata open directly into blood sinuses, which carry oxygen to all parts of the body. This is in contrast to lower types that have elaborate tracheal systems. This is evidence of specialization. Their eyes are compound, whereas all other centipedes have groups of ocelli, single ocelli, or none at all. This elaborate visual apparatus enables them to hunt successfully the flies and mosquitoes that are often present in dwellings, as well as the roaches and silverfish.

Specialized work on *Scutigera forceps* has been done by Duboisson (1928) who made a study of respiration and circulation and Cameron (1926) with respect to regeneration.

Unlike other centipedes, this species is not so rigidly bound by the need of a high relative humidity. The writer took one specimen inside of an electric light fixture in his home. This is an environment no other centipede could enter. This is rather the exception. Most members of this species are found in the basements or in dark corners of the house, or in spaces between the walls.

Although it is now commonly found in homes, it occasionally is still found in the natural environment. In this Area specimens have been taken among the rocks along the Chicago Drainage Canal.

Lithobius forficatus L., *Neolothobius voracior* (Ch.),
Bothropylus multidentatus (N.)

These three species are the centipedes most commonly found in the Area forests. Although they represent two families they are enough alike in appearance and general habits to warrant being treated under one heading. Phylogenetically *B. multidentatus* is considered the most primitive. Evidence of this is to be found in the increased number of tergites with posterior prolongations (6, 7, 9, 11, 13) as well as the multi-seriate coxal pores, and the shortness of the antenna (20 articles); *N. voracior* is intermediate in position with a decreased number of prolonged tergites (7, 9, 11, 13), a single series of coxal pores and an antenna increased in length (up to 36 articles); *L. forficatus* is the most specialized of the three with fewest number of prolonged tergites (9, 11, 13), single series of coxal pores, and most complicated antenna (up to 49 articles).

L. forficatus has been the subject of much investigation. Recently Thompson (1945) has written a short paper on the behavior of this species. Scharmer (1935) in an elaborate piece of work tested the responses of this species to such physical factors as light, such chemicals as amyl alcohol, clove oil, ammonia, musk, and H₂S. He also tested the animal in a T-shaped trough and found that the species could not adjust to the pattern even when shocked electrically, unless the walls of the pathway differed in texture. If the wall texture was changed, the animal manifested no directed response. According

to Scharmer the animal has a sense of smell dependent on the antennae—food, however, is not located by means of smell. In a temperature gradient the animal chose 27°C. It did not show any choice between moist and dry air in a T-apparatus. In a tube half of which had a moist substratum, the other half dry—the animals selected the moist half. Lichen (1943) studied relative growth in this species, while Needham (1946) utilized this species in studying the problems of variations in relative proportions in a series of similar structures.

Significantly, as will be dealt with in greater detail later on, and has already been indicated in the distribution pattern (Fig. 1), there is a difference in environments corresponding to this phylogenetic pattern. That is, *L. forficatus* is found in more xeric environments (dry forests, loose debris, under stones); *N. voracior* is found chiefly in a more mesic environment (intermediate forests); and *B. multidentatus* is found in the most mesic of environments (wet forests).

All three species are about the same size. Their coloration is similar—varying shades of reddish-brown that darkens with age and subsequent increased sclerotization. They seem to occupy the same niches in the forest communities, varying with the time of the year. That is, in the early spring with the forest floor damp as a result of the spring rains, they are chiefly found in the damp leaf mold, particularly in hollows where the mold is thick and wet. As summer approaches and the relative humidity of the forest community decreases the animals move into decaying logs and stumps. In mid-summer within the more xeric local communities, the animals retire deep beneath the surface of the ground or move into the interior of those logs that remain moist. Evidence supporting this observation is the fact that a damp log broken into at this time will usually yield large numbers of centipedes, whereas a similar log in the spring will yield only a few animals.

In the autumn, depending on the climate of the particular year, the animals either move out again onto the forest floor or remain restricted to their log habitats. With the onset of cold weather in mid-November or early December the centipedes move into hibernacular deep in logs, center of stumps, or in the soil itself, wherein they remain until spring.

The facts of reproduction in these species, as well as in the class as a whole, have been an enigma. Copulation has never been observed, although Heymons (1901) reported that he observed two scolopendrids which had their posterior extremities joined in a sort of complement. That copulation does take place is evinced by the fact that spermatozoa can be found within the reproductive tracts of the female.

The author tried to observe this phenomenon by pairing several specimens of *N. voracior*. Coitus was not observed although it possibly occurred as the female in one case laid a clutch of fertile eggs (No. 1, Table 2). The usual result of such pairings was that one of the two killed and ate the other.

TABLE 2. Period of oviposition of local lithobiomorpha.

Species	Date of Capture	Date of Oviposition	Number of eggs
No. 1. <i>Neolithobius voracior</i> (Ch.).....	May 31, 1947	July 7-13, 1947	38
No. 2. <i>Neolithobius voracior</i> (Ch.).....	June 20, 1947	July 17, 1947	1
No. 3. <i>Bothroplys multidentatus</i> (N.)....	July 5, 1947	July 9-10, 1947	3+
No. 4. <i>Bothroplys multidentatus</i> (N.)....	July 5, 1947	July 7, 1947	1+
No. 5. Lithobiidae sp.	May 1, 1947	July 24, 1947	1+
No. 6. <i>Neolithobius voracior</i> (Ch.).....	April 29, 1947	June 2, 1947	1+

Table 2 presents what data have been acquired in this study with regard to the time of oviposition of this group of species. Of these six observations only No. 1 is the result of what possibly was a laboratory mating. Both specimens were caught on May 31, 1947 and kept together until the female destroyed the male about July 4, 1947. Starting on July 7, eggs appeared between the female's gonopods and continued to appear through July 13, when a total of 38 eggs were counted. These were removed to a separate container and on July 28 the first of these hatched. Hatching continued through the month of August. Indications are, that at room temperature 24-25° C., the incubation period varied from 21 to 28 days.

The remainder of the data include specimens from three different communities. The specimens of *B. multidentatus* are from the Hemlock-Hardwoods community. The specimens of *N. voracior* (No. 2, No. 6) are from the Red Oak-Maple-Basswood community, and the Lithobiidae sp. is from an Oak-Hickory community in southern Indiana. Several important inferences can be drawn from these data. In five out of the six cases oviposition of centipedes occurred in July and the remaining female oviposited in June. In three cases the animals were in captivity over a month before oviposition took place. In No. 1 there is no positive evidence that the female was fertilized as a result of being placed with a male. It is equally possible that she already had been fertilized when caught. Specimens 3 and 4 were caught just prior to, or in the period of oviposition. If there is a definite period of oviposition as the data indicate it is reasonable to assume that there is a definite period of fertilization early in the spring or perhaps late in the autumn. Histological examination of the reproductive tracts of specimens taken during the late autumn and during the winter would undoubtedly go a long way towards answering this question. Whether this fertilization or rather impregnation is concurrent with egg maturation or whether it is simply a deposition of sperm within the tracts of the female which are utilized as each egg matures, is a matter of conjecture. Since the eggs are laid singly over a period of time (one week), the writer feels that the latter is closer to the truth.

Verhoeff (1925) believed that oviposition occurred at all times of the warm seasons. His reason for this was the fact that young centipedes could be caught at all times of the year. The present writer feels

that this is not quite the case. The evidence indicates that there is one period of oviposition in June or July, the dates of which depend, to a great extent, on previous climatic conditions. Hatching starts in August and continues into early September. The young go into hibernation as young (that is, without their adult complement of legs) and come out in the following spring, start feeding and molting and reach the imago state late in summer or early autumn. The group of *Neolithobius voracior* raised in the laboratory were still in an immature condition on November 27, 1947 when the last check was made. At this time centipedes of this species already would have moved into their hibernacula. My field observations have indicated that the peak of the young centipedes are found in the early spring and in late summer and early autumn (August-September). This agrees with the findings of Cole (1946a). That this long period between hatching and maturity is not too unusual and can be expected is further indicated by the long life of these animals. Verhoeff (1925) and Brolemann (1932) who cites Attems, maintain that these animals can live to a maximum of six years or more depending on the species.

Food habits also were investigated. The investigations were qualitative and the results on the whole are incomplete. Cole (1946a) reported that *Lithobius forficatus* feeds on Collembola. Verhoeff (1925) reported that the same species had difficulty catching Collembola even when placed in a tube of them. One immature lithobiid caught on July 5, 1947 was offered Acarina, and Collembola of the families Poduridae and Entomobryidae. It rejected the Acarina but took the podurid and apparently chewed on it for a time, and then rejected it. It accepted the entomobryid and ate it completely; then it caught another one that had crawled under its legs and devoured it. The lithobiid accepted and devoured a third offered with forceps. The centipede lunged at a fourth that had crawled under its legs, but missed, and ended chewing on a piece of soil. By making a sudden lunge the lithobiid finally caught another entomobryid that had touched its legs. After eating this last entomobryid it appeared to be satiated as it would not accept any more offered with a forceps.

In another case a large female *Neolithobius voracior* was offered a small spider which it took and ate. It subsequently rejected a podurid collembolan and a small staphylinid beetle. Another *N. voracior* was offered elaterid larvae which were never accepted.

The animals kept in the laboratory were maintained on a diet of dried earthworms; or in the case of the larger centipedes, small entire worms were given them. During the mayfly swarming period, which occurred during July, 1947, in Evanston, large numbers of mayflies were fed to the centipedes which usually did not hesitate to accept them. Muscoid flies also would be taken readily when proffered. Consequently the writer feels that these species (*L. forficatus*, *N. voracior*, *B. multidentatus*) will probably eat any small, soft-bodied form that they can catch.

Sonibius

Three members of this genus probably occur in this area. Two of these, *S. politus* and *S. numius*, have been taken by the writer. Figure 1 indicates that *S. politus* occurs in greatest percentage in the dry forests. The writer feels that further and more extensive collecting in the other communities will reduce this percentage. In a mesic community such as Warren's Woods where there are far more decayed logs and where conditions are moist throughout the summer, fewer animals were found per log, consequently fewer animals per collection. Whereas there are fewer moist logs in the local dry forests, the species may tend to be more concentrated.

The members of this genus are all small in size, the largest collected being 13 mm. in length, the average being 9.5 mm. Of these, *S. politus* comes closest to being one limited to a particular niche as described by Verhoeff (1925). They have always been taken in logs, particularly under bark when it could be peeled off. Holmquist (1928) in a study of arthropod hibernation indicates that this species tends to be gregarious. The present writer has found no evidence of this during the warm months of the year and has not been able to find any specimens at all during the winter, consequently the above observations can neither be confirmed or denied. Little else at present is known of their life history or habits.

Nadabius

Nadabius is another genus of small lithobiids. The largest specimen taken by the writer was 20.5 mm., the average being 12.5 mm. in length. Two species are reported from the area. One, *N. ameles* (Chamberlin 1944), described from a specimen taken in Dunes Park, Indiana, has never been taken by the writer. The other, *N. iowensis*, is one of the commonest centipedes in temperate North America. It forms 20% of the centipede population in the grassland in this area. It is also common in the forest communities, but here the figures are not accurate as it seems to be a leaf-mold inhabitant occurring in large numbers in the Beech-Maple and Hemlock-Hardwoods communities. Collections in the leaf mold of such small forms are limited to the results of a half-dozen Berlese samples.

Pokabius

Pokabius, represented by *P. bilabiatius* in this area and possibly by the subspecies *P. bilabiatius verdescens*, is very abundant throughout the Mississippi Valley (Chamberlin 1922). In the Chicago Area it has been collected only in the grassland (Fig. 1). South of here it has been taken in various forest communities. According to Chamberlin (1922) the genus has its center of origin in the Southwest, ranging up the West Coast and up the Mississippi Valley. His distribution map (p. 340) indicates that this is a prairie form as it follows the prairie peninsula pattern closely. Park, Auerbach & Wilson (1949) have found that *Reichenbachia subsimilis* (Casey), a pselaphid beetle found abundantly in

Peacock Prairie along with *P. bilabiatius*, has a distribution which indicates quite clearly a grassland origin. As far as *Pokabius bilabiatius* is concerned, extensive collecting in central Indiana and eastward through the prairie peninsula region is necessary to establish definitely this hypothesis. However, if such is the case, the presence of *P. bilabiatius* in the forests south of here would indicate either a successful invasion of the forest community which has not been accomplished in this region, or merely relict forms that have not been driven out by the new environment, or both. Schmidt (1938) has shown this to be possible in the case of prairie reptiles that remain as relict forms in the prairie peninsula all the way to western Pennsylvania. As with the other small Lithobiomorpha, details of life history and habits remain to be worked out.

Tidabius, Sigibius, Paitobius

These are genera of very small lithobiids averaging 8-9 mm. in length. Taxonomy of *Tidabius* and *Sigibius* is not yet on firm grounds (Verhoeff, 1925; Chamberlin, personal communication). Very few were taken in the present study and no data on them are available.

Otocryptops sexspinosus (Say)

This is the largest of the centipedes found in this area, over 40 mm. in length and possessing a bulky body. Being of the scolopendrid group it is more primitive than the previously discussed species. This is indicated by the increased number of body segments (23), absence of ocelli, shortened antennae, and the predominantly neo-tropical and tropical distribution of the order to which this species belongs.

Otocryptops is distributed all over the United States, being found from New York to California and from the Gulf coast to the Canadian border and beyond. With a distribution as widespread as this, it is not surprising that it occurs in all the forest communities in the Chicago Area. However, its habits are rather secretive and except during the breeding season and after periods of prolonged rainfall, specimens are found only in the most moist and most inaccessible habitats, such as deep in logs or stumps. During breeding or rainy periods they are much more prevalent. At this time they usually can be found under any piece of bark or wood, or in the top layer of leaf mold, or the loose mold of a stage V log.

In the literature this group is listed as feeding chiefly upon insects, spiders, worms, and smaller centipedes. Ten specimens of *O. sexspinosus* were kept at various times in the laboratory. These were both juveniles and adults. Seven of these ate earthworms readily. The other three did not live long enough for any prolonged observations to be made. Four specimens were available during the mayfly swarming period (July, 1947). Mayflies were taken and eaten by all four specimens.

There is more information available about this species' reproductive habits than there is for other Chilopoda. As mentioned previously, two members of

this order (Scolopendromorpha) have been seen in union. Whether or not this actually was sexual union was not definitely established at that time. Table 3 indicates the time of the year when members of this species were found with young and the number of such observed.

TABLE 3. Period of oviposition of Scolopendromorpha and Geophilomorpha.

No.	Species	Date caught with eggs or young	Number of eggs or young	Locality
1.	<i>Otocryptops sexspinosus</i>	June 18, 1948	49 eggs	Springport, Mich.
2.	<i>Otocryptops sexspinosus</i>	July 1, 1948	*20 eggs	Desplaines, Ill.
3.	<i>Otocryptops sexspinosus</i>	July 1, 1948	*10 eggs	Desplaines, Ill.
4.	<i>Otocryptops sexspinosus</i>	July 4, 1948	45 eggs	Desplaines, Ill.
5.	<i>Otocryptops sexspinosus</i>	Aug. 2, 1947	65 embry.	North Carolina
6.	<i>Otocryptops sexspinosus</i>	Aug. 2, 1947	65 embry.	North Carolina
7.	<i>Otocryptops sexspinosus</i>	Aug. 2, 1947	65 embry.	North Carolina
8.	<i>Otocryptops sexspinosus</i>	Aug. 18, 1947	157 young	North Carolina
9.	<i>Otocryptops sexspinosus</i>	July 24, 1947	52 eggs	North Carolina
10.	<i>Otocryptops sexspinosus</i>	June 27, 1947	38 embry.	North Carolina
11.	<i>Geophilus rubens</i>	Aug. 1, 1948	60 embry.	Saugatuck, Mich.
12.	<i>Geophilus rubens</i>	Aug. 1, 1948	25 embry.	Saugatuck, Mich.
13.	<i>Geophilus rubens</i>	Aug. 1, 1948	25 embry.	Saugatuck, Mich.
14.	<i>Geophilus rubens</i>	Aug. 1, 1948	27 embry.	Saugatuck, Mich.
15.	<i>Geophilus rubens</i>	Aug. 1, 1948	26 embry.	Saugatuck, Mich.
16.	<i>Geophilidae</i> sp.....	June 3, 1947	unknown	Southern Indiana

*Adults may have eaten some of the eggs before the count was taken.

†Young were 8 mm. in length.

The data on oviposition are not as exact as in the case of the Lithobiomorpha (Table 2). The northern forms of Scolopendromorpha seem to have oviposited from the middle of June into the early part of July, which compares favorably with the Lithobiomorpha of this area. The North Carolina specimens, a gift of Dr. Nelson W. Hairston, all had broods that ranged from eggs to hatched young. Close examination of the data suggests that they also fall within the June-July ovipositing period. Cornwall (1934) found *Scolopendra viridis* Say and *Cryptops hyalinus* Say, both members of this order, with young or with eggs during June or July in the Duke University forest (North Carolina). Field observations indicate that in this group juveniles are most abundant in the early autumn and in the spring, signifying, as with the large Lithobiomorpha of this area, a period of one year or more before the imago state is reached.

In this order (Scolopendromorpha) as well as in the most primitive order of centipedes (Geophilomorpha) the phenomenon of "brooding" is common. This is in contrast to the precocious development of the young of Lithobiomorpha and probably of Scutigleromorpha. The mother *O. sexspinosus* stays with the eggs until they are hatched and with the young until they can fend for themselves. If the female is disturbed it is probable that she will eat the eggs. The eggs themselves cannot be incubated away from the female. Brolemann (1932) states that the female keeps the eggs raised off the ground by coiling her body around them. If perchance an egg should drop out of the clutch, it is abandoned and is shortly destroyed by fungi or other microorganisms. The

writer agrees in essence with this, but in a few cases he has observed "brooding" females moulting some of the eggs. It is possible that by so doing she may be coating the eggs with a fungicidal secretion as is done by certain species of ants. Moreover, if an egg is dropped it is not abandoned in the anthropomorphic sense, but rather it is a case of not knowing and not being able to detect such a loss. The susceptibility of the eggs to microorganisms is very great, entire clutches being obliterated in two or three days in damp soil within the laboratory. The average number of eggs per clutch (Table 3) is 46, with a higher number in the southern members of this species. This compares favorably with the 15 to 33 per clutch for *Scolopendra* by Heymons (1901).

Two other species of this order have been reported from this area, namely, *Cryptops hyalinus* Say and *Theatops spinicaudus* (Wood). One specimen of the former was taken at Saugatuck, Michigan by the writer. The latter species was reported by Wood (1863), but never has been reported since.

Geophilus rubens Say

This is the largest species of this order (Geophilomorpha) in the Chicago Area. It belongs to the most primitive of the chilopod orders. Its many body segments (49-53), lack of ocelli, and short antennae, as well as its "brooding" habits attest to this primitive condition. It ranges in length up to 60 mm. and 1-1.5 mm. in width. *Geophilus rubens* is identified readily by the darkish stripe down the middle of the dorsal surface. It is commonly found under the bark of dead trees or logs. Like *O. sexspinosus*, this species is found in all forest communities studied and is common throughout north-eastern United States. Its local distribution is still obscure.

Reports in the literature from Newport (1844) and Wood (1865) to date, state that earthworms form the diet of this group. In the laboratory the writer was not able to convince himself of the validity of this. In practically all cases, entire worms or parts of worms were ignored. One geophilid caught on May 31, 1947 took no food all summer. On September 5, 1947 it was offered a piece of worm which it took, chewed on for a short while, and then stopped feeding and crawled away. Collembola were offered but were rejected. The same results were obtained when mites, small beetle larvae, and small spiders were tried. Much more work along this line is needed.

As stated before, "brooding" is also characteristic of this order. Data found in this study (Table 3) indicate that the average number of eggs per clutch is about 33, which compares favorably with Verhoeff's findings of 19 to 30 in this group, depending on the species. Oviposition, as in the other orders, takes place in June or July. Hatching takes place in August and early September. Little field data are available on the immature forms so no hypotheses can be drawn as to the length of their development from juvenile to imago.

Arenophilus bipuncticeps (Wood)

This geophilid species occurs in this area in the grassland where it forms 23% of the centipede population. It, too, is an ubiquitous species throughout the Northern United States. However, not enough data are available to indicate whether it might be a true prairie type as *Pokabius bilabiatu*s or a forest type that has secondarily invaded the prairie. Chamberlin (1912) found members of this species with eggs on June 22, 24, and 26, 1910, indicating that it also oviposits during the same time as other local members of its class. As previously stated it also enters the ant nests of *F. ulkei* E. and other species; but its relationships with the ants have never been worked out.

Linotenia

Two species of this wide-spread genus are found abundantly in the Chicago Area, viz., *Linotenia fulva* and *Linotenia chionophila*. Both are predominantly leaf mold inhabitants, only occasionally are they taken in logs. Their small size and light-reddish color makes their detection difficult in hand sorting of leaf mold. Berlese samples of leaf mold from all the forest communities in the Chicago Area yield these species.

One specimen of *L. fulva* was offered various kinds of food. These included two species of beetle larvae, Collembola, mites, and some ptiliid beetles. Of these one small beetle larva was eaten. Pieces of earthworm were not eaten. No reproductive data were found for these centipedes.

Other species of Geophilomorpha were taken (Table 1); and although they are undoubtedly present in considerable numbers, not enough were taken to indicate either the pattern of their distribution or any of their habits.

RELATIVE HUMIDITY STUDIES

All previous workers in the chilopod group have commented on the importance of relative humidity in the distribution of these animals—distribution in the sense that they are for the most part, restricted to niches in which there is a high relative humidity. The present writer, in three years of field observations, has found nothing to contradict this view. The one exception to this, in this area, was *Scutigera forceps*, previously mentioned.

The idea, however, of moisture being an important factor in zoogeographic distribution of chilopod species has never been investigated. This is not surprising in view of the fact that the study of the rôle of various physical factors in the distribution of animals is still in its infancy. Moreover, it remains to be demonstrated quantitatively how important a single factor may be in affecting the distribution of animals.

These investigations resulted from some earlier work (Auerbach 1949), in which three species of centipedes were subjected to gradients of relative humidity. The three species responded differentially and quantitatively to the gradient. However, no conclusions could be drawn regarding their distribution

as they all came from the same forest. The three species (*Bothropylus multidentatus*, *Neolithobius voracior*, *Otocryptops sexspinosus*) are common in this area and the differences in distribution of the first two that became apparent after the first year of field work indicated that an investigation of the humidity responses of these and other local species might give some clue to the rôle of humidity.

METHODS AND MATERIALS

Two types of experiments were performed. The first and the greater part of the experimentation consisted of subjecting the animals to desiccation conditions. The desiccation technique was used by Gunn (1935) in a study of three species of cockroaches. He compared the rates of desiccation in dry air at various temperatures and found that there are clear specific differences. Hairston (1949) who used the same type of technique on three species of salamanders, found a difference in the rate of desiccation which showed a correlation with the animals' natural environments. Secondly, some humidity gradient experiments were performed. These experiments were not quantitative, but rather were relative in nature.

Desiccation experiments of two kinds were done. First a series of experiments were performed using the technique set forth by Park, Allee, & Shelford (1939). These consisted of placing the animals in petri dishes, the bottoms of which were covered with dry filter paper, and allowing them to desiccate at room temperature and room relative humidity. Controls were placed in the same type of dishes. In this case, the bottoms were covered with moist filter paper. This technique is open to criticism, chiefly because there is no constant humidity. The room relative humidity varied at least 10% from day to day as the experiments were carried on.

To correct for this, another method was tried; a modification of the apparatus used by Rilett (1946). Instead of petri dishes a series of small constant humidity chambers were set up. The bottoms of these chambers were filled with a water solution of sulfuric acid (Wilson 1921) which maintains a definite and constant vapor pressure and—as a result—a characteristic relative humidity. The chambers in this case were small laboratory desiccating jars. Fine copper screening resting on a lead tripod above the solution provided a place for the animals. Sulfuric acid of a density of 1.35 grams per cubic centimeter gave a relative humidity of 35% at 23° C. For controls, water instead of acid was placed in the bottom of the chambers.

In both sets of experiments animals were placed within the chambers within two days after capture in order to minimize the starvation factor. In such cases where the animals could not be utilized so rapidly, they were kept in the refrigerator at a temperature just above freezing in order to keep their activities at a minimum.

Apparatus designed after that of Lunn (1939) was used for the humidity gradient experiments. This was a strip of brass 15 inches in length (Fig.

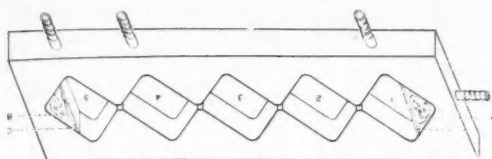


FIG. 2. Humidity gradient apparatus designed after that of Lunn (1939). A—wet sponge, B—dry sponge, C—screening, 1-5—gradient chambers.

2). Five communicating compartments, each 50 x 50 x 18 mm. were cut in the plate (1-5, Fig. 2). Communicating passageways between the compartments were 5 mm. wide. A series of pipes led from the compartments to the outside. These were used to insert the animals and then sealed. A glass plate, sealed with vaseline, formed the cover.

In order to establish a humidity gradient a wet sponge was placed in Chamber 1 (A of Fig. 2), and a dry sponge was placed in Chamber 5 (B of Fig. 2) in order to make Chambers 1 and 5 alike except for the humidity. Pieces of fine screening (C of Fig. 2) prevented the centipedes from crawling into the sponges. The apparatus was allowed to stand thus for two hours before animals were put into it by means of one of the outlet pipes. It can again be emphasized that this apparatus merely establishes a relative diffusion gradient, not a quantitative humidity gradient in a measurable sense.

EXPERIMENTAL RESULTS, HUMIDITY GRADIENT

The results of the humidity gradient experiments are summarized in Tables 4, 5, and 6. In these experiments four or five animals were used at a time in the apparatus. In the third group (Table 6) the three common lithobiid species are represented. The reason for this is that the animals were placed in the chambers without being identified. This was done to minimize handling them—thus lessening the possibility of doing them some bodily injury. It will be noted that this latter group manifested a greater relative response to the moist end of the gradient than did those of *Neolithobius voracior*.

TABLE 4. Response to moisture of groups of *Neolithobius voracior* (average of 6 experiments of 5 centipedes each).

Time	PERCENT OF ANIMALS IN CHAMBERS				
	Wet 1	2	3	4	Dry 5
After 5 min.	53.3	6.6	3.3	16.6	20.0
10 min.	56.6	6.6	0.0	16.6	20.0
20 min.	56.6	13.3	0.0	16.6	13.3
30 min.	53.3	16.6	3.3	16.6	10.0
40 min.	60.0	16.6	3.3	13.3	6.6
50 min.	60.0	13.3	6.6	10.0	10.0
60 min.	53.3	16.6	16.6	6.6	6.6
90 min.	53.3	20.0	10.0	6.6	10.0
120 min.	60.0	20.0	10.0	0.0	10.0
150 min.	60.0	20.0	10.0	0.0	10.0

TABLE 5. Response to moisture of groups of *Otocryptops sexspinosus* (average of 5 experiments of 5 centipedes each and one of 4 animals).

Time	PERCENT OF ANIMALS IN CHAMBERS				
	Wet 1	2	3	4	Dry 5
After 10 min.	55.2	6.9	3.4	13.8	20.6
20 min.	58.6	10.3	6.9	0.0	24.0
30 min.	65.5	10.3	6.9	3.4	13.8
40 min.	72.4	6.9	6.9	3.4	10.3
50 min.	79.4	3.4	10.3	3.4	3.4
60 min.	87.4	4.2	0.0	0.0	8.4
90 min.	75.0	8.4	4.2	4.2	8.4
120 min.	79.0	10.5	0.0	5.2	5.2

TABLE 6. Response to moisture of mixed groups of one *Lithobius forficatus*, one *Bothropylis multidentatus*, and two *Neolithobius voracior* (average of 2 experiments of 4 animals each).

Time	PERCENT OF ANIMALS IN CHAMBERS				
	Wet 1	2	3	4	Dry 5
After 5 min.	62.5	0.0	0.0	12.5	25.0
10 min.	87.5	0.0	0.0	0.0	12.5
20 min.	100.0	0.0	0.0	0.0	0.0
30 min.	87.5	12.5	0.0	0.0	0.0
40 min.	100.0	0.0	0.0	0.0	0.0
60 min.	100.0	0.0	0.0	0.0	0.0

and *Otocryptops sexspinosus*. The data are insufficient to draw any specific conclusions, but they do indicate the relation between Chilopoda and moisture, as well as the possibility that there is a species differential in response to moisture.

EXPERIMENTAL RESULTS, DESICCATION

The question of the acid vapors affecting animals was examined by Gunn (1937), in his study of the humidity reactions of the woodlouse. He performed three like experiments using substances other than sulfuric acid, but having the same vapor pressure. His results with these were the same as those with the acid. He concluded, therefore, that the responses of the animals were responses to humidity and not chemical stimulation. In view of these results this desiccation technique was used to study differences in survival between species of centipedes.

Six species of centipedes were utilized in the preliminary experiments. The results are summarized in Table 7. The various desiccation death times were plotted as cumulative frequency percentages and smoothed (Fig. 3). These show a decided difference in death times between *Otocryptops sexspinosus*, *Neolithobius voracior*, *Lithobius forficatus*, and *Bothropylis multidentatus*. The last, *B. multidentatus*, has the shortest survival time. These results were the first clue as to the possibility of moisture playing

a rôle in the differential distribution of *L. forficatus*, *N. voracior* and *B. multidentatus*. In the earlier work (Auerbach 1949), *B. multidentatus*, in the humidity gradient, spent 47% of the time in the moist portion and 31% in the intermediate area, while *N. voracior* spent 34% in the moist portion and 50% in the intermediate zone. No work with *L. forficatus* was done. In these experiments, utilizing desiccation instead of humidity response, *N. voracior* seems to have a longer survival time than *B. multidentatus*, while that of *L. forficatus* is still greater than the preceding two.

TABLE 7. Desiccation experiment: temperature 20-23° C.; relative humidity 20-40%.

Species	Number of animals used	Average length (mm.)	Mean death time (hours)
<i>Sonibius politus</i>	4	10.0	2.7
<i>Pokabius bilabiatu</i> s.....	5	12.0	2.4
<i>Bothroplys multidentatus</i> juv....	5	11.0	2.8
<i>Bothroplys multidentatus</i> adult.	12	18.0	4.0
<i>Neolithobius voracior</i> juv.....	5	14.0	4.6
<i>Neolithobius voracior</i> adult.....	10	20.0	5.9
<i>Lithobius forficatus</i> juv.....	9	12.0	3.9
<i>Lithobius forficatus</i> adult.....	8	21.0	9.3
<i>Otocryptops sezspinosus</i>	4	30.0	15.7

Another problem, however, was posed by these results, that of the size factor in relation to desiccation. As can be seen (Fig. 3) *O. sezspinosus*, the largest of the local centipedes, which in this case averaged over 30 mm. in length, had a far greater survival time than any of the other species tested.

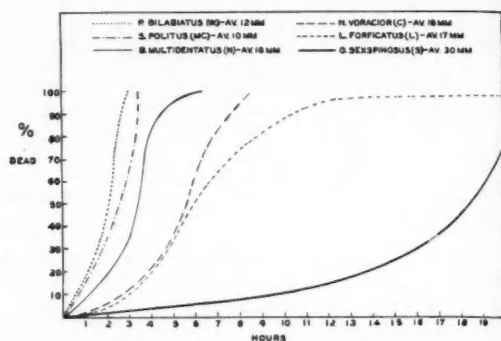


FIG. 3. Death times of certain centipedes desiccated in petri dishes. Curves are smoothed cumulative frequency percentages.

This is strictly in accord with the Spencerian surface-volume principle, namely, that surface increases by the square, whereas volume increases by the cube, so that the larger individuals within a species would survive longer because their evaporation surface per unit volume would be relatively less than that of the smaller individuals.

If there is an intra-specific as well as an inter-specific difference in death time due to size, what bearing has this on the hypothesis that moisture, or a lack of it, is a possible limiting factor in the distribution of *N. voracior*, *B. multidentatus*, and *L. forficatus*? First of all it is necessary to show that there is a correlation between size and desiccation death time. Figure 4 is a scatter diagram in which body-length is plotted on the ordinate and desiccation death time on the abscissa. This graph was based

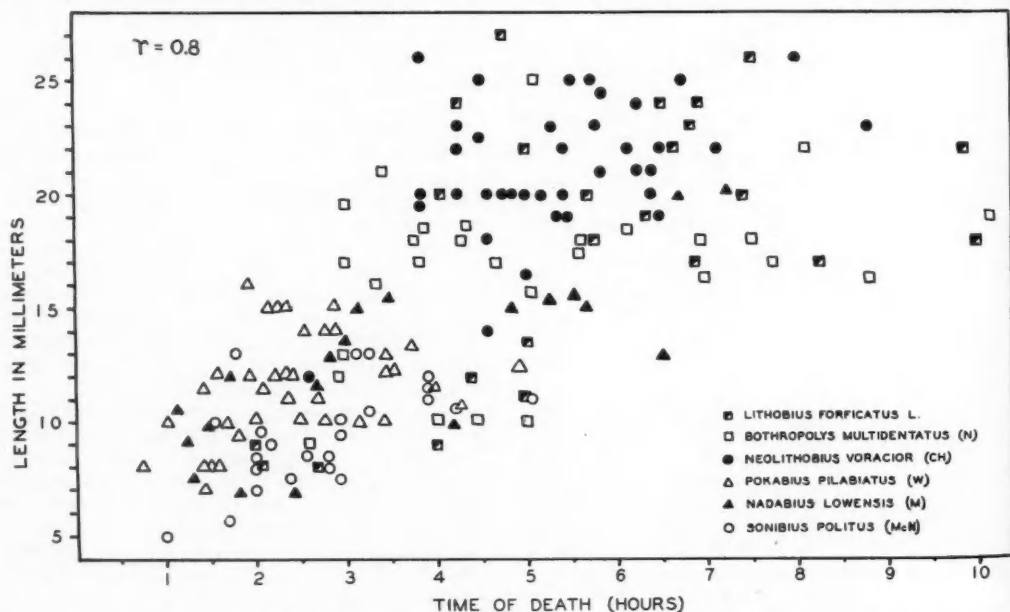


FIG. 4. Scatter diagram illustrating the relationship between body-length and desiccation death time.

on the data of the second set of experiments. The correlation between body-length and desiccation is quite evident. Graphically it shows a correlation coefficient about 0.8. Mathematically, utilizing the arithmetic means, it had a coefficient of 0.914.

Secondly, it is necessary to show that there is an intra-specific difference due to size. Consequently the data of the three species in question were divided and plotted as follows:

<i>B. multidentatus</i>	av. length 11 mm. and 18 mm.
<i>N. voracior</i>	av. length 14 mm. and 20 mm.
<i>L. forficatus</i>	av. length 12 mm. and 21 mm.

Figure 5 contains the plottings, and supports the Spencerian principle as well as the moisture hypothesis. *B. multidentatus* has the shortest survival time for both small and large individuals. The survival curves of the small individuals of *N. voracior* and *L. forficatus* are about the same. Here the larger average size of *N. voracior* may be a factor in the closeness of fit of these two curves. Finally, the large individuals of *N. voracior* and *L. forficatus* exhibit a decided difference between their curves of survival.

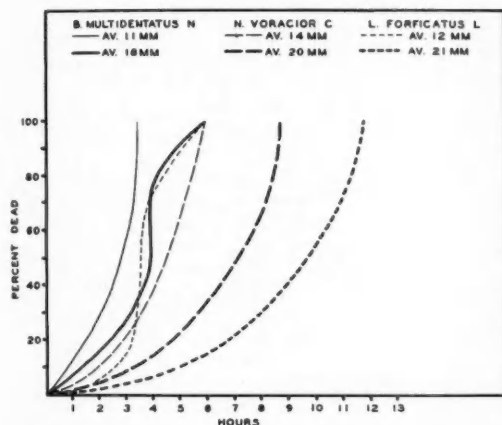


FIG. 5. Desiccation death times of three species of centipedes divided into adults and juveniles. See Fig. 3 for curves of the same species *in toto*.

The second set of desiccation experiments are summarized in Table 8. In this series, enough animals were used to treat the data statistically. In the case of the three species mentioned above *B. multidentatus* had a mean death time (adult) of $5.4 \pm .44$ hours; *N. voracior* had a mean death time of $5.5 \pm .18$ hours; and *L. forficatus* $6.6 \pm .40$ hours. Of these, only *L. forficatus* proved to be significantly different from the other two species. In the case of the juveniles *N. voracior* had the greatest survival time, followed by *B. multidentatus* and then *L. forficatus*. Here again the smaller average size of *L. forficatus* juveniles may have been a causative factor. Although the data here do not unequivocally support the hypothesis (for reasons which will be dealt with later), the same trend is apparent.

TABLE 8. Desiccation experiments; temperature $22.5-25^{\circ}\text{C}$; relative humidity 35%.

Species	Number of animals used	Average length (mm.)	Mean death time (hours)	Coef. Var. (%)	Stand. Dev. in Hours
<i>S. politus</i>	26	9.4	$2.7 \pm .13$	24.8 ± 3.5	$.67 \pm .09$
<i>P. bilabiatu</i>	42	11.2	$2.4 \pm .11$	30.5 ± 3.5	$.74 \pm .08$
<i>N. iowensis</i>	20	12.8	$3.4 \pm .29$	38.7 ± 6.9	$1.32 \pm .21$
<i>B. multidentatus</i> Juv.....	10	12.8	$4.5 \pm .59$	40.0 ± 10.4	$1.83 \pm .41$
<i>B. multidentatus</i> Adult.....	19	19.0	$5.4 \pm .44$	35.6 ± 6.5	$1.91 \pm .31$
<i>N. voracior</i> Juv.....	4	14.1	$4.7 \pm .71$	30.0 ± 11.5	$1.45 \pm .50$
<i>N. voracior</i> Adult.....	36	21.8	$5.5 \pm .18$	20.0 ± 2.4	$1.11 \pm .13$
<i>L. forficatus</i> Juv.....	7	10.5	$3.6 \pm .50$	32.6 ± 9.6	$1.18 \pm .32$
<i>L. forficatus</i> Adult.....	17	21.3	$6.6 \pm .40$	25.0 ± 4.5	$1.65 \pm .28$
<i>A. bipuncticeps</i>	22	37.2	$7.3 \pm .36$	23.1 ± 3.5	$1.70 \pm .25$
<i>O. scapinosus</i>	22	38.0	$11.2 \pm .85$	35.8 ± 5.9	$4.00 \pm .60$
<i>G. rubens</i>	7	43.0	27.8 ± 1.7	16.9 ± 4.6	4.71 ± 1.2

The smaller Lithobiomorpha present some interesting results. The prairie species, *P. bilabiatu*, in both sets of experimentation had the shortest survival time (av. length 11.2 mm.; $2.4 \pm .11$ hours). Shorter in both cases than *S. politus*, the small forest species (av. length 9.4 mm.; $2.7 \pm .13$ hours). The same results were obtained with the prairie and forest geophilids. *Arenophilus bipuncticeps*, the prairie species, lasted $7.3 \pm .36$ hours; while *Geophilus rubens*, the forest species, survived 27.8 ± 1.7 hours. Here we have results in which species (*P. bilabiatu*, *A. bipuncticeps*) of an exceedingly xeric environment (prairie) die in a significantly shorter time than forest members of the same size category.

The use of body length as a variable in this type of investigation has been questioned. Body weight has been suggested as a better criterion. Table 9 contains the weights of some typical species of centipedes used in the desiccation experiments. Referring to this table and to Table 8 it will be seen that *G. rubens* with an average length of 43.0 mm. has the longest survival time (27.8 ± 1.7 hours) and the specimens weighed had an average length of 58 mm. and average weight of 0.043 gms. Comparing these centipedes with those of *B. multidentatus* adults (19.0 mm., $5.4 \pm .44$ hours) the weights of which within this length category range from 0.05 gms. to 0.09 gms., it is evident that the longer, lighter type has by far the greater survival time. However, another type of result is obtained when the larger prairie species *P. bilabiatu* is compared with the smaller forest species *Sonibius politus* (Tables 7 and 8). In this case the longer and heavier body type has a shorter survival time than the lighter and shorter type. Therefore, as far as the adults are concerned, indications are that some mechanism is operative which controls water loss by the animal, and is, in the majority of cases, correlated with body length (Fig. 4).

In the case of the juveniles (Tables 8, 9), the juveniles of the larger species, *L. forficatus*, *B. multidentatus*, and *N. voracior*, while being of the same length as adults of smaller species (*P. bilabiatu*, *N. iowensis*) are heavier in weight and have a longer survival time. A possible reason for this is that the

TABLE 9. Some weights of certain Chicago Area centipedes.

Species	Sex	length (mm.)	Weight (gr.)
<i>Geophilus rubens</i>	f.	61	.052
<i>Geophilus rubens</i>	f.	52	.030
<i>Geophilus rubens</i>	f.	62	.049
<i>Otocryptops sezzpinosus</i>	—	46	.207
<i>Otocryptops sezzpinosus</i>	—	38	.1099
<i>Otocryptops sezzpinosus</i>	—	40	.1065
<i>Bothropyls multidentatus</i>	m.	19	.0585
<i>Bothropyls multidentatus</i>	f.	22	.0925
<i>Bothropyls multidentatus</i>	f. imm.	9	.0257
<i>Bothropyls multidentatus</i>	f.	21.5	.0794
<i>Nadabius iowensis</i>	f.	12	.0184
<i>Nadabius iowensis</i>	f.	10	.0080
<i>Nadabius iowensis</i>	f.	8.5	.0051
<i>Pokabius bilabiatu</i> s.....	f.	8.5	.0097
<i>Pokabius bilabiatu</i> s.....	m.	12.5	.0154
<i>Pokabius bilabiatu</i> s.....	m.	7.0	.0143
<i>Pokabius bilabiatu</i> s.....	m.	15.0	.0224
<i>Pokabius bilabiatu</i> s.....	m.	10.5	.0096
<i>Pokabius bilabiatu</i> s.....	m.	9.7	.0079
<i>Pokabius bilabiatu</i> s.....	f.	13.0	.0152
<i>Pokabius bilabiatu</i> s.....	m. imm.	8.5	.0049
<i>Pokabius bilabiatu</i> s.....	m. imm.	7.5	.0031
<i>Pokabius bilabiatu</i> s.....	m. imm.	7.5	.0033
<i>Sonibius politus</i>	f.	10.0	.0085
<i>Sonibius politus</i>	m.	10.0	.0093
<i>Sonibius politus</i>	f.	7.0	.0026
<i>Sonibius politus</i>	f.	6.5	.0019

greater bulk of the juveniles actually presents a smaller evaporating surface than that of adults of a smaller species.

The bearing of these results on the hypothesis that moisture is a limiting factor in the distribution of local species of centipedes will be treated in the discussion.

POPULATION INVESTIGATIONS

The quantitative study of soil faunas is strictly a 20th Century product. The earliest of these investigations was made by Diem in 1903 at various altitudes in the Alps. His studies, like the majority of those that followed, dealt with entire soil populations. Among the latter are those of McAtee (1907) who investigated the fauna of four square feet of forest and meadow near Washington, D. C., Dammernan (1925, 1937) who made studies in various islands of the East Indies, Grimmer (1926) who made a study of the floor fauna in a mixed rain forest and southern beech forest in New Zealand, Weese (1924), who reported on the fauna of an Illinois elm-maple forest. All of these authors used some modification of the hand-picking method.

The Berlese funnel, or some modification of it, has been used effectively in the study of quantitative soil populations. Pillai (1921), using a Tullgren funnel, studied the litter of a pine forest. A German pine forest was also studied by Pfitzen (1925); monthly collections were made and treated in a

Tullgren funnel. Trädgårdh (1928, 1933) reported studies on the soil fauna of Swedish forests. Bornebush (1930) made an extensive study of the soil fauna of Danish forests. American workers include Jacot (1936a, 1936b), Lunn (1939), Williams (1941), and Pearse (1946).

The only long-term analysis of a natural population known to the writer is that of Shelford (1947). This study covers all strata of a forest community for a period of sixteen years, and is being continued.

Prairie quantitative studies were inaugurated by McAtee (1907). European workers have been particularly active in studying this type of biotic community. Cameron (1917) studied the insect fauna of a meadow. The insect fauna of arable land was studied by Morris (1920). Dogel (1924) worked on the fauna of a meadow. In 1937 Wolcott made a study of a meadow and a pasture in northern New York. Thompson (1924) made a survey of a permanent pasture. Ford (1937, 1938) studied the fluctuations in natural populations of Collembola and Acarina from a meadow. A comparison of the fauna of different types of pasture-land was made by Edwards (1929).

Within more recent years the trend has been toward the analysis of particular taxonomic groups of organisms. The Acarina and Collembola because of their great population density have perhaps been more studied than others. Many of the above authors, for example, have given especial attention to this group.

The use of quantitative population figures over a period of time, however, has been little used in the working out of life history relationships. The majority of studies have dealt with total population fluctuations, ratios of various species populations, aspeotional changes, soil sterilization, grazing, plowing, etc. The present study, on the other hand, was mainly concerned with getting at the dynamics of the centipede population, and by so doing, maybe get some insight into their yearly life history relations. Similar treatment has been given to beetles of the widely distributed family Pselaphidae (Park, Auerbach, & Wilson 1949, 1950) and to the Pauro-poda (Starling 1944).

AREA OF STUDY

Two biotic communities were utilized in the analysis of the soil population of centipedes. These were Carlé Woods—a Red Oak-Sugar Maple-Basswood forest; and Peacock Prairie, a patch of undisturbed prairie.

Carlé Woods is located fifteen miles west of Evanston, Illinois on the Desplaines River, just north of U. S. Highway 58. This forest has been the site of ecological community studies by Lunn (1939), Strandine (1939), and Daggy (1946).

Peacock Prairie is a typical prairie border area with a thick, rich prairie soil. It is of swamp origin as was much of the original prairie in this area. Characteristically, it contains a great many forbs with only a few grasses. Figure 6 shows the typical aspect of the prairie during midsummer. Its vege-



FIG. 6. Typical midsummer aspect of Peacock Prairie as seen from the west.

tation and moisture relationships have been elucidated by Paintin (1929). Park, Auerbach, & Wilson (1950) have made preliminary studies on the dynamics of the pselaphid beetle population of this grassland.

With the exception of this latter work and the yearly cutting of a small patch of low grass for fodder, as well as some burning, the prairie has remained undisturbed. Since Paintin's original description there has been no indication of any change in the vegetation to indicate a trend from prairie to forest; consequently it can be assumed that this will remain as one of the prairie border interdigitations formerly so common in this region.

METHODS AND MATERIALS

Starting October 20, 1947, Berlese samples were taken once a week for a year, the last collection being made on November 24, 1948. During the period January 14-March 22, 1948, a sudden drop in the temperature froze the soil so that no samples could be taken. This period of extreme cold was followed by a record snowfall which rendered both research areas inaccessible for some weeks.

A very simple method was utilized for obtaining the samples. A metal quadrat frame 0.08 m² was placed on the ground, the leaf mold was first removed from within it and placed in a sack. Then the soil was dug out to a depth of four inches and placed in a can. Soil temperature was taken at the same time with a Taylor soilpoint thermometer. No attempt was made to separate the vegetative matter from the soil in the prairie sample. One sample was taken from each area every week. The samples from Peacock Prairie had an average weight (dry) of 4700 grams. The soil samples from Carlé Woods had an average weight (dry) of 4400 grams.

In the laboratory the soil was placed in a battery of Berlese funnels and dried out under a 40-watt bulb for two days. After this time, except with the leaf mold, a 100-watt bulb was used. The samples were heated constantly, because the rather large amount of soil dried out slowly; as the soil dried it was removed from the funnel. This enabled the writer to complete one sample from each area per week.

During the winter of 1947-48 a series of 12 boards

were placed on the ground at Peacock Prairie. These were so arranged that they occupied ground of varying levels. Their original purpose was to serve as "traps" for centipedes needed for experimental work. Beginning on April 1, however, records of the number under each board were taken each time a soil sample was removed. These provided another series of quantitative data. Since these board niches (cryptozoan niches, Cole 1946a) provide an environmental complex quite different from that within the prairie soil, the data will be dealt with separately.

RESULTS

The totals of the weekly collection were made for each month, and the monthly totals were divided by the number of collections made. This gave an average figure for each month (Table 10). The total average population for the year is also shown.

The field work indicated that general climatic conditions play an important rôle in the fluctuations of the population. To test this situation the monthly populations of Peacock Prairie and Carlé Woods were plotted against precipitation, mean air temperature (obtained from the Monthly Climatological Survey of the United States Weather Bureau) and soil

TABLE 10. Average monthly populations per square meter.

Month	Peacock Prairie	CARLÉ WOODS		
		Leaf Mold	Soil	Total
November 1947	25	5	18	23
December	25	0	32	32
January 1948	13	0	0	0
February	omitted	6	6	12
March	omitted	13	0	13
April	25	8	5	13
May	50	0	13	13
June	25	6	6	12
July	19	19	0	19
August	38	0	30	30
September	31	3	5	8
October	13	6	5	11
November	35	0	0	0
Total average number per square meter . . .	27	5	9	14

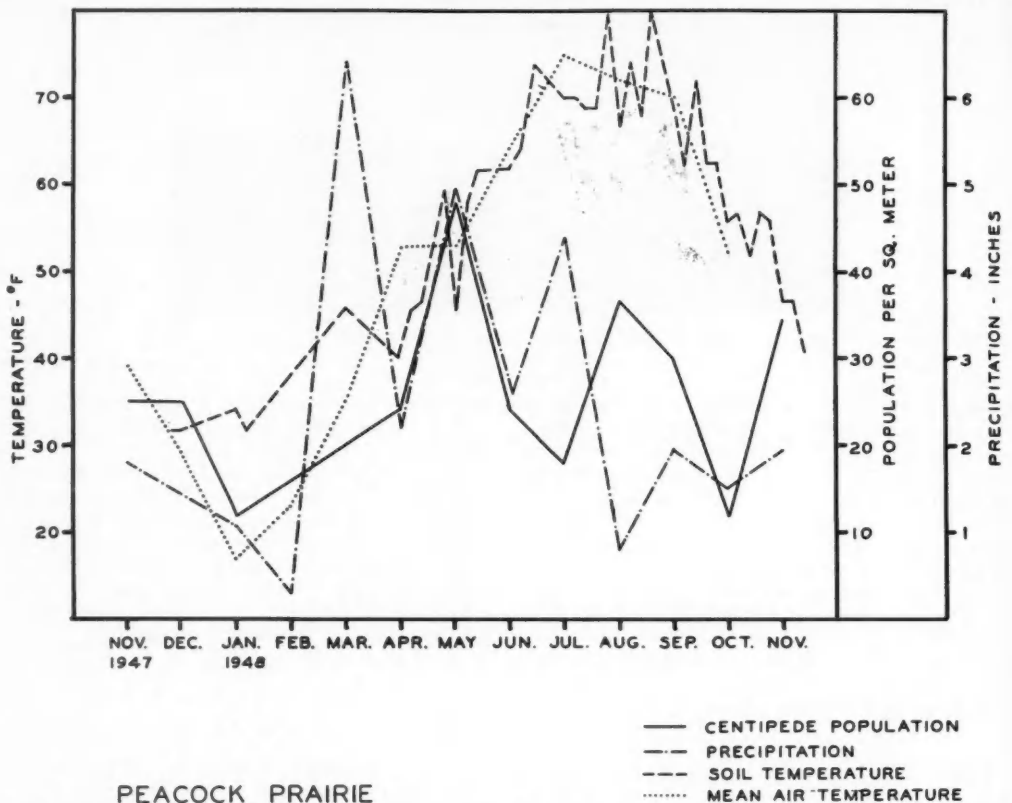


FIG. 7. Graph showing the fluctuations of the prairie centipede population in relation to certain environmental factors during the period of study.

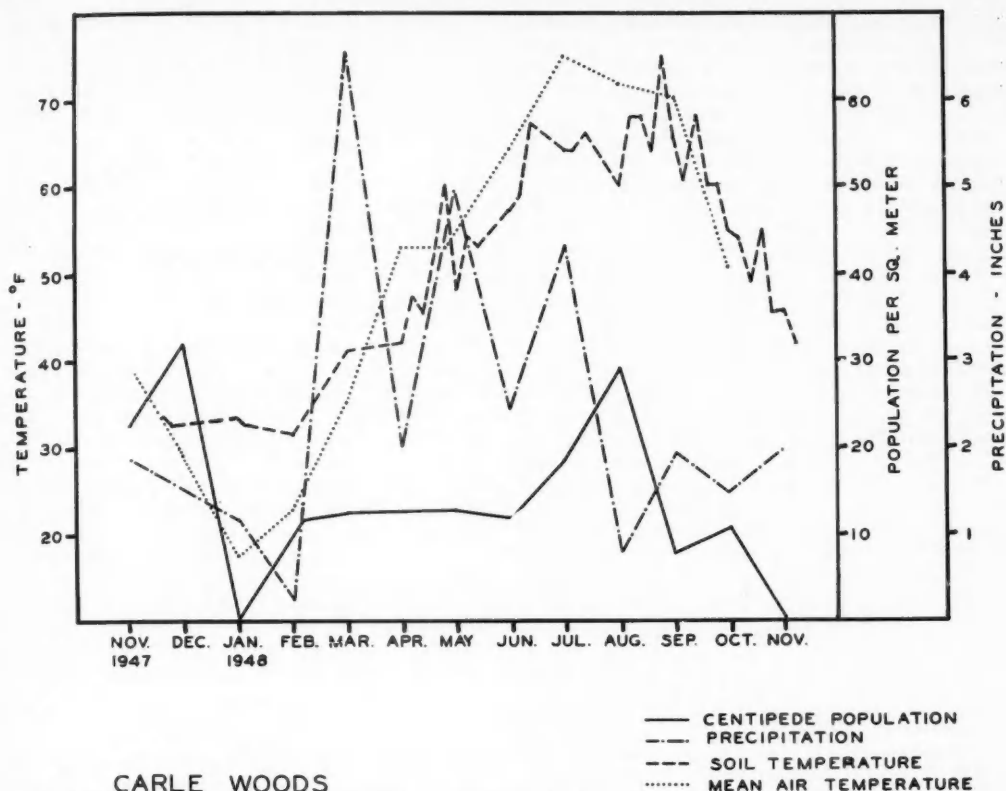
temperature taken at each collection. The mean air temperatures were obtained by totaling and averaging the daily means for the period between, or prior to, each collection. The precipitation was obtained by totaling the daily precipitation for the same time. It is possible that by means of this method the rôle of a climatic complex operating on a particular Berlese collection may be indicated.

Although the mean air temperatures were calculated from temperatures taken at the Chicago Municipal Airport, some twenty-five miles from Peacock Prairie and Carlé Woods, the curves (Figs. 7, 8) follow the soil temperature curve. This is both interesting and relevant since in some measure it suggests that the use of the weather bureau data is justified. In the open prairie the soil temperatures were higher, generally speaking, at the time of collection (Fig. 7). In the forest with its insulating canopy and greater floor litter the soil temperature tended to be lower than the mean air temperatures (Fig. 8).

None of these data are critical. They indicate a general relationship between the climate and the monthly population averages. In the late autumn, at the start of the collections, a relatively high population was found both in the forest and the prairie.

With the onset of winter and very low temperatures there was a decided drop in population, which denoted a movement into hibernacula out of the reach of the collector. Dowdy (1944a), in a study of the effect of soil temperature on the movements of soil animals, found that during the winter there is a definite downward movement into the soil directly correlated with soil temperature. Included in his finds were three species of centipedes also found in this area, namely, *Arenophilus bipuncticeps*, *Nadabius iowensis*, and *Geophilus rubens*. More recently Salt, Hollick, Raw, & Brian (1948) in a study of the arthropod population of pasture soil found that the difference in numbers of *Geophilus* in collections made in May and November was statistically significant. The authors suggest that *Geophilus* may move up and down in the soil in correlation with different seasons of the year.

In the Chicago Area, with the onset of warm weather and spring rains, beginning in April, there was an upsurge in the prairie centipede population that reached its peak in May. Following the May high in precipitation (Fig. 7), the June precipitation decreased. At the same time the soil and mean air temperatures continued to rise. Although the soil temperatures were in the vicinity of 60° F.,



CARLE WOODS

FIG. 8. Graph showing the fluctuations of the forest centipede population in relation to certain environmental factors during the period of study.

it should be noted that these readings were taken in the morning and that they would be considerably higher in the afternoon. The apparent effect of these conditions on the centipede population is indicated by the progressive decrease in abundance of prairie centipedes in June and July. In the prairie it is apparent that following the July peak in precipitation there is an increase in the August population. But during July and August the high air temperatures dry the top soil very rapidly. The high soil temperatures (80° F.) of July and August are only attained under arid conditions. All these conditions would tend to reduce the population density. Consequently this August peak may represent the addition of young which hatch at this time.

August precipitation was low (less than 1 inch), accompanied by a rather high mean air temperature and high soil temperature. The population dropped off sharply in September in the prairie. With the advent of the autumn rains, plus moderate temperatures, the prairie population showed a close response to climate, rising to an average of 38 per square meter for the month.

In the forest the centipede population reached a plateau in March and maintained it through May (Fig. 8). This population stability may be due to

the fact that the forest floor niches are all moist. This provides more habitat niches for centipedes to occupy. The moist condition tends to be maintained by the canopy which insulates the forest floor against external environmental conditions. Consequently the monthly population of March, April, and May (Fig. 8) may be the minimum floor population in Carle Woods at this time of the year. Any increase in numbers at this time would possibly represent individuals moving in from other niches (for example, logs and stumps). A decrease in numbers may be a consequence of the operation of environmental conditions that would place individuals of the population at a soil level that is relatively out of reach of the collector. The latter condition is probably the cause of the decrease in the June population (Fig. 8). That is, there was a decrease in precipitation which probably was little if at all effective because of the maximum foliation of the canopy. July witnessed a rise in population along with an increase in precipitation and the population peak was attained in August. This latter increase probably represented the increment that resulted from the hatching of the young. In the forest the population dropped off sharply in September. Dowdy (1944b), in a study of population fluctuations in a disturbed

deciduous forest area, found that *Geophilus strigosus* (McNeill), one of the predominant organisms and one of the common centipedes in that area, had two peaks in population density during the year both in the forest and in open areas. One was in the vernal period (April 21-June 18) and one in the hiemal (November 30-March 15). The Carlé Woods population continued to drop in the autumn. This is possibly due to the fact that during this period the soil and leaf mold of the woods were not appreciably moistened by the rains.

The close response of the prairie species may be the reason underlying the experimentally demonstrated fact that the prairie centipede fauna does not survive desiccating conditions as long as forest centipedes of the same or shorter body lengths. The prairie species may be so well adjusted to the extremes of prairie environments that they are more sensitive to climatic changes, and move quickly up

and down in the soil in response to such changes. This sensitivity, then, may be demonstrated in the lesser ability of these species to withstand desiccation as compared with the forest species that occupy niches where relative humidity is almost constant throughout the year.

In spite of prairie centipedes being more responsive to general climatic conditions than are forest species, their average population (Table 10), is almost twice that of Carlé Woods, being 27 to 14 per square meter. However, centipede populations in different types of communities may vary greatly as several authors have demonstrated (Table 11). Some of these investigators have divided their figures on a square foot or square meter basis, or multiples thereof. In order to compare their findings the present writer recalculated these figures on population density per acre basis. The writer does not consider these figures definitive in any sense, agreeing with Buckle (1923, p. 99), "except where there is a pronounced infestation, the estimate of numbers per acre has purely a fictitious value." For purposes of comparison the reduction to a common population denominator has value. Another important point is that many of these authors were interested in the whole soil population and the relative fractions of its components. Consequently they gave no particular attention necessarily to each group. This may give rise to a considerable error under certain conditions of collecting.

Thirdly, the methods of collecting, as well as the size and number of samples differed with each study. The British group (Buckle 1921, Thompson 1924, Morris 1927, Edwards 1929, and Baweja 1939) used a nine-inch cube of soil which usually was broken down and sorted by hand. Some of these authors did not separate Chilopoda as a definite group or did not obtain enough data to handle them quantitatively. Other authors (Pearse 1943, Hayward 1948) used the hand-picking and sorting method, usually doing it in the field, while Salt, Hollick, Raw, & Brian (1948) used a sieve-floatation technique. Still others (Bornebusch 1930, Starling 1944) used the Trädgärth, Berlese, Tullgren, or Silvestri funnel method.

In spite of these possible sources of error it seems that as the community becomes richer in organic materials there is an increase in centipede population. Of course this is concomitant with a general increase in population for that area, as examination of the authors' complete figures will reveal. An exception to this is in the figure of Bornebusch for Beech, raw Humus II. In this category he obtained 273 geophilids (1,104,000 per acre) per square meter. He calls attention to this fact because all other population groups showed a decrease in this area. It is possible that he sampled some sort of aggregation which accounted for the unusually high figure. Salt, Hollick, Raw, & Brian's (1948) figures of 432 centipedes (1,750,000 per acre) per square meter for the lower six inches of pasture soil is very likely due to an aggregative condition, because, as they say (p. 148), "on the basis of coefficients of dispersion, and

TABLE 11. Comparative number of centipedes in thousands per acre.

Morris 1927	
Arable Land	
Undunged.....	3.0
Dunged.....	134.0
Bornebusch 1930	
Beech, mull I.....	315.5
Beech, mull II.....	28.3
Beech, mull III.....	32.3
Beech, impoverished soil.....	113.2
Beech, raw humus I.....	84.9
Beech, raw humus II.....	1104.5
Oak, mull.....	121.3
Spruce, mull.....	141.6
Spruce, raw humus.....	198.2
Spruce, raw humus.....	473.3
Eaton & Chandler 1942	
2nd growth beech, ash, oak.....	54.4
2nd growth red maple, beech.....	653.4
50 yr. beech, maple, ash.....	54.4
Red oak, beech, maple, ash.....	271.7
Pearse 1943	
Lobolly Pine	
Intact.....	43.3
Burned over.....	1.4
Raked.....	0.7
Dowdy 1944b	
Potentilla-Solidago-Rumex.....	7.7
Solidago-Agrostis-Daucus.....	13.4
Quercus-Carya.....	13.4
Acer-Tilia-Sambucus.....	13.1
Fagus-Acer.....	10.3
Starling 1944	
Pine stand on sand.....	261.3
Oak stand on sand.....	217.8
Hayward 1948	
Wasatch Chaparral	
Open area.....	4.8
Under oak.....	17.4
Salt, et al., 1948	
Pasture soil	
Upper 6 inches.....	875.0
Lower 6 inches.....	1750.0
Auerbach present report	
Carlé Woods.....	56.6
Peacock Prairie.....	109.2

as far as the collections go, it appears that a non-random aggregated distribution is common to several groups of soil arthropods" (centipedes were one of these groups). It also should be noted that these authors made a much more thorough sampling during their two-month analysis than did any of the other workers cited.

Morris' (1927) figures for "dunged" and "undunged" arable land are strikingly different. The addition of organic material resulted in a tremendous population increase which is reflected in the increase of centipedes. Conversely, Pearse's (1943) removal or burning of the humus of the forest floor results in a decrease in floor population with the centipede population following the same trend.

Fluctuation of centipede population is strictly in accord with the pyramid of numbers concept as enunciated by Elton (1927) and the biomass concept of Pickles (1937) and numbers concept of Ghilarov (1944). Centipedes are large invertebrate predators intimately linked within the community food web where they feed on a larger group of herbivores and small predators. A diminution of the numbers of the herbivores should result in a decrease in the number of predators. It is not surprising that where the centipede population fluctuated from one area to another, either as a consequence of natural or artificial causes, their relative numerical proportion to the rest of the animal population remained essentially the same, with the exceptions noted previously.

BOARD ANALYSES

Cole (1946a) in his excellent paper on the "eryptozoan fauna" presents various statistical approaches for the analysis of distribution of animals under boards. The present writer set out twelve boards at random in Peacock Prairie in order to obtain centipedes for laboratory experiments. Exact records were kept of the number of chilopods taken under each board and the amount of moisture on the underside of the board was subjectively estimated at that time.

When these data were tabulated, enough had been assembled to warrant statistical treatment similar to that of Cole's. However, certain differences between the studies must be noted. First, Cole did his studies in woodlots. The species of centipedes he found were *Lithobius forficatus*, a non-prairie form; and *Arenophilus bipuncticeps*, a common prairie inhabitant, but rarely taken under the boards at Peacock Prairie. Secondly, the present writer began his systematic board observations in April, carrying them on through the summer and autumn. Only scattered observations were made during the winter as the boards were usually frozen to the ground and when they were not, no animals were found. Thirdly, two species of centipedes were found together under the boards at Peacock Prairie. These were *Pokabius bilabiatus* and *Nadabius iowensis*, of which the former constituted 71% and the latter 29% of the total number. There is no way of rapidly identifying them at sight.

If animals are distributed at random, the numbers

in field experimental areas should correspond to a Poisson distribution (Cole 1946a). Cole never found *L. forficatus* common enough to test their distribution, except in the winter when he found them in aggregations which, as he says (p. 71), "certainly indicates a non-random distribution for at least a part of the year." He tested other species of animals (millipedes, sow bugs). These he found did not correspond to a Poisson distribution, whereas spiders so tested did.

In the period April-November, 1948, 444 observations were made of the boards in Peacock Prairie (Table 12). There were 176 centipedes noted in these observations and distributed as shown. Their distribution does not conform to the Poisson distribution, and indicates therefore, a non-random dispersion. Testing this by means of the Chi-square method confirmed this non-random distribution. Figure 9 shows this pattern plotted as a curve. The centipede distribution crosses the Poisson at about two centipedes per board.

TABLE 12. Distribution of centipedes under boards.

	NUMBER OF CENTIPEDES PER BOARD					
	0	1	2	3	4	5
Observed frequencies	339.0	67.0	21.0	10.0	2.0	5.0
Expected (Poisson)	298.7	118.3	23.6	3.0	0.3	0.02

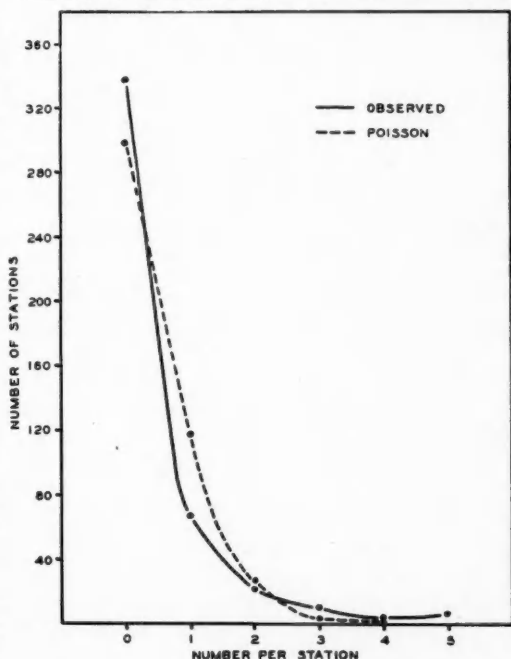


FIG. 9. Distribution of centipedes under boards at Peacock Prairie. "Contagious" distribution of Cole (1946a, b).

Another statistical means of indicating a possible aggregating tendency is the Charlier coefficient of disturbance. Beall (1935) found it to be a very satisfactory index of aggregating propensity. It is written as $C = \frac{100 s^2 - x}{x}$; where s^2 is the standard deviation of the distribution and x represents the mean catch. Positive values of C indicate aggregation, whereas C becomes imaginary with overdispersion. Testing the centipede distribution by this method gave a Charlier coefficient of 2000+. This may be construed to indicate a definite aggregation.

Cole (1946a) feels that this aggregating tendency is not merely response to environment as he says (p. 72), "Although soil moisture, and perhaps additional undetected factors, may lead to contagious distributions under the conditions of this study, it seems probable that a considerable part of the aggregating tendency observed is attributable to a mutual attraction between members of the same species," and (p. 75), "this complicated behavior of the isopods, leaving shelter and moving to boards harboring larger numbers of isopods, as well as the vertical migration from unfavorable conditions, suggest that the complexity of aggregation phenomena has been underestimated in attempts to reduce these phenomena to mechanical responses such as altered rates of turning" (Waloff 1941).

It seems to the present writer that if aggregation is to be defined in terms of distribution there must be a third category in addition to random dispersion and mutual attraction. Cole (1946b) speaks of this third category as a "contagious" distribution, the cause of which can be any number of biotic and physical factors, mutual attraction being only one of these causes.

The greatest number of centipedes under boards occurred in April and May when the prairie soil and the boards were saturated with moisture. During the summer there was a decided drop in numbers which was maintained through most of the autumn. Although systematic winter observations were not made, the writer made casual examinations during the winter of 1947-48. At that time the boards in many cases were frozen to the ground and could not be lifted. In those instances where they could be, the undersides of the boards were covered with frost or a thin film of ice and no animal life was detected.

The presence of moisture as a possible operative factor in the centipede distribution was noted by the writer every time regular observations were made. If the boards were dry underneath, as most of them were during summer, animals were rarely present. If they were partly wet and centipedes were present, these were almost always found in the wet portion of the board. Table 13 contains the results of 515 observations in which records were kept of centipedes found under boards and the conditions of the boards at the time of observation.

It is apparent that there is a close relationship between the board moisture conditions and the number of animals present. Unfortunately no measurements

TABLE 13. Distribution of centipedes under boards in relation to moisture; 515 observations. Dry—no moisture on board; part wet—moisture on one or more parts of board; wet—board wet throughout.

	BOARDS		
	Dry	Part wet	Wet
Number of centipedes observed	5	41	130
Number of observations where no centipedes were observed	215	45	79

of soil moisture were made under the boards. Nevertheless it was noted that the latter were never wet unless the soil beneath them was wet. A rainfall after a period of warm dry weather necessarily did not cause the boards to become moist underneath, although the soil around them was moist. Only after the ground was thoroughly soaked and not dried out too rapidly did the boards become moist again. Cole notes that his isopods tended to form larger aggregations as the soil became more moist. Although the present writer took no count of prairie isopods, his observations corroborated those of Cole's. But, when the boards were moist and many isopods were present, there were also many centipedes present.

If the conditions under the board were of a favorable nature, biotic or otherwise, it might be assumed that the number of animals under a plank would be large in an especially favorable period, i.e., larger than the number of animals in an equivalent amount of soil. The average area of one of them was 0.25 m² and at no time did the average number of centipedes under that amount of surface exceed the average number in the soil for the same period.

A hitherto unmentioned factor can be noted, although its relationship to this problem is still obscure, namely, the time of collection and the condition of the animals at that time. Collections were made during the day and the great majority of centipedes observed were relatively inactive ("sleeping?"). Their bodies were so curved that the anterior end almost met the posterior end. If the day was overcast and cool, they made no effort to move unless prodded, after which they straightened and moved rapidly off the board. On the other hand, when the day was bright, the sudden appearance of light seemed to stimulate them, i.e., they moved rapidly off the board. It may be that this "cryptozoan" niche is frequented by centipedes during the night in search of food and that those found there during the day were there when the sleep-producing factors became operative, and remained there because moisture conditions were suitable.

In view of all this the writer is inclined to believe that the appearance of two or more centipedes under the boards (Fig. 9) is not necessarily an aggregative condition.

Several criticisms are germane. The fact that the centipedes found under the boards represent a heter-

ogeneous sample may be a serious cause of error. One species probably has a behavior pattern which is entirely different from another. Another possible source of error is that the boards were in prairie areas that varied in the amount of soil moisture content at the same time of the year. This was minimized by observing all twelve of the boards whenever possible. Third, observations were made only during a part of the year. If the observations had been carried out for a twelve-month period it is within the realm of possibility that the distribution under that greater number of observations might conform to that of Poisson.

STUDIES OF HEART BEAT

In the course of these investigations on Chilopoda it was observed that the heart was readily visible through the dorsal surface of the animal and its pulsations were easily counted. The heart of chilopods was probably first described by Newport (1843). The heart extends throughout the length of the trunk just beneath the dorsal surface. Ostia are present in each definitive segment. The branches consist of lateral segmental arteries and an anterior aorta. A pair of anterior arteries surround the gut and join ventrally to form the supraneural artery. Occasionally the heart is not visible; this occurs in old animals where the chitin is thickened and darkened.

The physiology of arthropod circulation has been discussed by Maluf (1939). The references to work on Chilopoda are few and the mechanism of its circulatory apparatus can only be arrived at by inference. The present writer's studies were strictly of a preliminary nature and were not concerned with the mechanism of circulation.

METHODS AND MATERIALS

Simple apparatus was used in these studies. Ordinary petri dishes of both small and large sizes were provided with a glass collar made out of a short piece of 10 mm. glass tubing fused to an opening in the side of the dish. This collar provided an opening and support for a thermometer which was inserted in the dish with the animal. By this means the temperature of the microclimate in which the animal was resting was obtained at the same time that the heartbeats were recorded. The bottom of the dish was covered with damp filter paper. The centipede was placed in the apparatus which in turn was placed under a dissecting microscope. The animal was given enough time to adjust itself to its new surroundings, i. e., coming to rest in a particular portion of the dish. Light provided by a Burton microscopic lamp was filtered either through a water bath when a constant temperature was desired, or allowed to illuminate the apparatus directly when an increase of temperature was necessary.

The method for obtaining the heartbeat count was as follows. Each systole was counted as one beat. A series of beats were counted, the number depending on the rapidity of the systolic rhythm. The time for these was read with a stopwatch. Readings were taken continuously for at least a 30 minute period;

usually a 60 minute period was employed. These readings were totaled and averaged and the average rate per minute determined for a particular temperature.

RESULTS

"The heart rate varies with numerous factors such as general metabolic rate, fatigue, stretch, and the presence of various agents in the blood. Even under apparently identical conditions the heart rate of different individuals of a given species and age varies considerably. In a given individual under normal conditions, however, the rate is fairly constant although the frequency of the periodic arrests which occur in certain species is very variable" Maluf (1939, p. 260). The present writer has also found in the case of centipedes that size, expressed as body length is also a factor in heartbeat rate.

Heartbeat rates of various local species were taken (Table 14). Other conditions being equal, the longer the animal the slower its rate of heartbeat. A notable factor is its close correlation with temperature. A difference of two or three degrees Centigrade results in a corresponding increase or decrease of the rate regardless of the species. Nevertheless there is an indication of a species difference in rate of heartbeat. Many additional experiments using animals kept under constant culture conditions are needed to confirm this.

The close relationship to temperature indicated the possibility of making some observations on the rate of heartbeat in relation to relatively large changes in temperature. The effect of varying temperature on the rate of biological processes has been much studied. The basis for this was the hope that an investigation of the temperature coefficient of a process might furnish a clue as to the real nature

TABLE 14. Comparative heart beat rates.

Species	Length (mm.)	Beats (min.)	Temp. (°C.)	Time
<i>Geophilus rubens</i>	—	33	24.5	9:15- 9:40 P.M.
<i>Geophilus rubens</i>	—	25	28.0	10:15-11:15 A.M.
<i>Geophilus rubens</i>	50	30	27.8	9:05- 9:40 P.M.
<i>Linotenia fulva</i>	—	27	24.0	9:40-10:35 P.M.
<i>Linotenia fulva</i>	—	38	27.0	2:20- 2:55 P.M.
<i>Theatops posticus</i>	41	46	28.0	11:00 A.M.
<i>Theatops posticus</i>	18	76	31.8	2:55- 3:22 P.M.
<i>Theatops posticus</i>	41	44	26.4	7:05- 8:15 P.M.
<i>Otocryptops sexspinosus</i>	19	77	25.0	2:30- 3:20 P.M.
<i>Otocryptops sexspinosus</i>	40	54	25.0	4:15- 5:30 P.M.
<i>Bothriophys multidentatus</i>	21	118	27.3	8:15-11:15 P.M.
<i>Bothriophys multidentatus</i>	—	126	31.0	4:15- 4:45 P.M.
<i>Neolithobius voracior</i>	—	105	31.5	3:20- 4:15 P.M.
<i>Neolithobius voracior</i>	27	100	29.0	3:50- 4:15 P.M.
<i>Neolithobius voracior</i>	25	61	26.0	2:30- 3:05 P.M.
<i>Neolithobius voracior</i>	28	90	28.0	10:50-11:25 P.M.
<i>Lithobius forficatus</i>	26	83	24.6	3:15- 3:50 P.M.
<i>Lithobius forficatus</i>	—	85	29.0

of the phenomenon. Such a hope has been realized to a limited extent.

Table 15 contains the Van't Hoff (1884) Q_{10} of the heart rates of some species of centipedes. In order to obtain temperature differentials, the previously noted apparatus was heated by means of the microscope lamp or cooled by means of ice. Unfortunately at temperatures above 35° C. the animals became too restless to obtain readings; below 8° C. water condensation on the glass of the apparatus prevented seeing the heart. Between these two extremes a large enough range existed to provide enough data to calculate a tentative Q_{10} . As can be seen (Table 15) there is a difference in Q_{10} at different ranges. At the lower ranges the Q_{10} tends to be higher, which is to be expected, as a process that is almost inhibited by low temperatures would of course have a high temperature coefficient, whereas, processes at temperatures above the optimum would decrease as the thermal death point was approached, with a consequent lowering of the Q_{10} . It is of interest that in the higher temperature ranges (Table 15) the Q_{10} is in the vicinity of 1.5 rather than the traditional 2. The experimental data are not sufficient to warrant any conclusions with respect to the significance of this observation.

TABLE 15. Q_{10} for various centipedes.

Species	Temp. range, °C.	Q_{10}
<i>Theatops posticus</i>	10-20	1.56
	20-31	1.63
	26-36	1.57
	10-36	1.56
<i>Bothropolys multidentatus</i>	14-24	3.19
	14-28	2.42
	18-28	1.43
<i>Otocryptops sexspinosus</i>	23-33	2.32
<i>Linotenia fulva</i>	24-28	3.77

DISCUSSION

LOCAL DISTRIBUTION

In the Chicago Area it has been shown that there are thirty known species of centipedes divided among twenty-one genera. These embrace populations that are adjusted to forest conditions, others that are adjusted to prairie conditions, still others that are adjusted to both forest and grassland, and one at least, that is found almost entirely in the houses of man.

With respect to the forest habitat three species of centipedes were given especial attention since they demonstrated a differential distribution as between forest types, the details of which could be subjected to laboratory analysis under controlled conditions. These three species populations are, *Bothropolys multidentatus*, *Neolithobius voracior*, and *Lithobius forficatus*. *B. multidentatus* is the most primitive of the three, *L. forficatus* is the most specialized, and

N. voracior occupies an intermediate position. Their distribution in the Chicago Area would seem to follow this phylogenetic pattern. In this study *B. multidentatus* was in greatest abundance in the forests that would be considered the most primitive if the age of the trees, amount of disturbance, number of fallen trees, and thickness of leaf mold are criteria. *N. voracior* was found most abundantly in forests that are predominantly second growth but have a thick canopy, a distinct layer of leaf mold, and whose floor niches are moist during part of the warm season. *L. forficatus* was found chiefly in the most disturbed forest areas, i. e., areas that in many cases could hardly be called forest at all. It was found also in such non-forest niches as backyard woodpiles, under and among the rocks in gardens, and beneath railroad ties. An outstanding physical differential between these several environments is the decreasing amount of moisture present. It was this apparent relationship between species population density and conditions of moisture that suggested a possible experimental analysis.

The greatest source of error in the study of local distribution may be the collecting techniques employed. Shelford (1913a) speaks of a standard mode or pattern of collecting, to be followed in each locale. This entails, as far as the Chilopoda are concerned, investigating to the same degree the niches where centipedes are usually found. Lowrie (1942), in a study of xeric duneland spiders, felt that the number of trips on which a given species was collected is a better criterion for their abundance than the number of animals collected. However, he was working chiefly in one type of habitat and, furthermore, was interested in the abundance of different species in that particular community type. Where several types of communities are being investigated the writer feels that the first method, that is, the relative abundance of different species based on a standard collecting pattern, is sufficiently accurate to obtain valid results.

Unfortunately, the Chicago Area is the only region in which centipedes have been collected with the object of determining their distribution on a broad, ecologic basis. Consequently, there is no evidence with which to contrast the distribution of these three species in North America as a whole. Moreover, both *B. multidentatus* and *L. forficatus* are very abundant throughout the eastern United States, and *L. forficatus* is also abundant in Europe. The published records contain so little ecologic information that the validity of the distribution of these centipede populations is difficult to judge.

Other members of the class are distributed broadly throughout the area, with the exceptions of prairie and social niches. Here too, *Nadabius iouensis*, which is found in the prairie, is also found in the forests (Fig. 1). The other two prairie species, *Pokabius bilabiatatus* and *Arenophilus bipuncticeps*, are apparently limited to grassland only in the Chicago Area. In the case of *P. bilabiatatus*, the evidence deduced from a reinterpretation of Chamberlin's data (1922) indicates that it is a prairie species and that its

occurrence in southern forests is a secondary invasion of a new habitat. With respect to *A. bipuncticeps*, all evidence suggests that it is a widely dispersed population and is successful in a great variety of habitats.

The zoögeographic problem is made more difficult in that in the United States many common northern or northeastern genera are not found in the Chicago Area. In addition certain species spend a part of their life span in ant nests. This adds to the complexity of the problem. Nevertheless, the results of the physiologic experiments indicate that the distribution noted previously is plausible. The application of such experiments as well as additional field data should yield gratifying results on a broader zoögeographic basis.

BIOLOGY

The present investigation has shown that oviposition in three of the four orders of Chilopoda occurs in June or July. The notes in the literature (Chamberlin 1912, Brolemann 1932, Cornwall 1934) substantiate this conclusion. If such is the case, the young, which emerge in about three weeks or more, come out at that time of year when climatic conditions are unfavorable to their survival, i. e., during the hottest period of the summer (late August and early September). It is probable, although the evidence is not yet forthcoming, that the late summer droughts may be a limiting factor on the size of the centipede population. Field collecting shows these young in abundance all through the autumn. Winter collecting has not been profitable, but collections as early as March have yielded young lithobiids. It is these juveniles, together with the adults that survive the winter, that make up the minimum centipede population. During spring and the following summer the young begin molting and may become adult during the summer. There is no direct evidence to substantiate this, and it may be that they do not attain sexual maturity until the following year, i. e., two years after hatching. The problem is complicated by the fact that centipedes are relatively long-lived and that little information is available on growth in relation to time. Many centipedes in this area survive for over a year. The writer has taken large lithobiids (*Neolithobius voracior*, *Lithobius forficatus*) in the spring. Since these were of maximum size for the species and were heavily sclerotized, as evinced by their dark coloration, the writer feels that they were over two years old. This belief is based on the findings of European workers (Verhoeff 1925, Attems 1930) who have found that centipedes can live six years or more, depending on the species involved.

RELATIVE HUMIDITY STUDIES

Cain (1944) in speaking of plant distribution says (p. 17), "physiological processes are multi-conditioned, and an investigation of the effects of variation of a single factor, when all others are controlled, cannot be applied directly to an interpretation of the rôle of that factor in nature." Whereas this generalization may apply to plants, there is an impressive

amount of documentation on various animals that indicates that single factor analysis, while not as satisfactory as the possession of complete information, is helpful. In fact, the complete study is rare in ecological investigations.

Humidity has been one of the chief factors investigated with reference to distribution. An early work on this factor was that of Shelford (1913b) who subjected two salamanders of the genus *Plethodon* to a humidity gradient and found that *P. glutinosus* is more sensitive to dry air than is *P. cinereus*. This is correlated with habitat differences since *P. glutinosus* lives in more damp places than does *P. cinereus*. The results are interesting in that *P. cinereus* is usually the smaller animal, and its relative evaporating surface per unit weight would be greater.

Talbot (1934) found that there was a physiological difference in survival time to desiccation for various species of ants in the Chicago Region. She believed that these differences were probably adaptive in that they correlated with the ability of the species to penetrate niches where the moisture supply at times may be very low. Williams (1934), experimenting with two species of termites, *Reticulitermes hesperus*, characteristic of more moist regions, and *R. tibialis* of more arid places, found that the former would not survive as long as the latter in soil with little moisture.

Granted that there is a differential in distribution of the three centipede species, *Lithobius forficatus*, *Neolithobius voracior*, and *Bothropolys multidentatus*, that corresponds roughly to the general moisture conditions of the forests where each predominates, it may still be asked, what importance does relative humidity play in this distribution? If centipedes spend the greater part of their lives in conditions that are always humid, how could relative humidity be a factor tending to limit the range of distribution of one species? Specifically, why should *B. multidentatus* always be found in the logs of an undisturbed climax forest such as Brownfield Woods (Auerbach 1949) while *L. forficatus* is rarely found there? In the dry, open, disturbed woodlots found so frequently in the Chicago Area, *L. forficatus* is the predominant species while *B. multidentatus* is scarce.

With regard to the rôle of humidity, one is dealing with two different species, each of which is a member of a different family. *B. multidentatus*, as stated earlier, is the more primitive of the two species and, while widely distributed in eastern North America, its distribution is nowhere as great as that of *L. forficatus*. The latter is found over most of North America and much of Europe. In the Chicago Area there is a difference in their local distribution that is correlated with the moisture conditions of their habitat niches. Consequently, the fact that they are taxonomically distinct, with all that this implies in physiological requirements, may account for their distribution.

Perhaps the most important evidence indicative of the rôle played by humidity, or its related factors

such as saturation deficit and evaporation, is that of definite receptor mechanisms present in a variety of arthropods. As Dethier & Chadwick (1948) state (p. 231), "many aspects of hygrostimulation are so strikingly reminiscent of olfaction that water vapor cannot be denied the rôle of a chemical stimulus solely on the basis of its omnipresence in the environment."

Blumenthal (1935) has identified both anatomically and experimentally humidity receptors on the legs of spiders. Pielou (1940) has found the humidity receptors for *Tenebrio molitor* L. These are probably pit-peg organs and peg organs on the antennae. Wigglesworth (1941) proved that the humidity receptors of the human louse are distinct from the olfactory receptors. Both are borne on the antennae. Lees (1943) found that the humidity receptors of wireworms of the genus *Agriotes* are located on the head, and that they are distributed on the antennae, and on the maxillary and labial palps.

Additional studies that correlate the humidity response of animals with their distribution in nature include those of Allee (1931) and Gunn (1937) on terrestrial isopods. Gunn compared the rate of water loss per hour for *Porcellio scaber* (Latreille) against that of the mealworm (Buxton 1930) and the cockroach (Gunn 1933), and found that *Porcellio* had a statistically significant higher rate and died in a few hours. Gunn (1935) found species differences in rate of desiccation of three kinds of cockroaches, and these differences were ecologically correlated. Gunn & Pielou (1940) found that the mealworm beetle, *T. molitor* L., responded significantly to the drier side of a humidity chamber that contained two different relative humidities. Lees (1943) found that wireworms responding closely to the saturation deficit of the air, tend to avoid dry air. He states (p. 53), "Wireworms avoid dry air, the intensity of avoidance being greatest when the alternatives are close to saturation. Within this humidity range a difference of 7.5% R.H. in the alternative chamber (at 17° C.) is sufficient to ensure the successful avoidance of the lower humidity by nearly every individual, while statistically significant reactions are The behaviour can readily be correlated with the humidity conditions prevailing in the soil; the necessity for such a sensitive response is possibly dictated by the permeability of the cuticle which renders wireworms peculiarly liable to water loss in unsaturated atmosphere."

In view of the fact that so many different groups of animals have been shown to have humidity receptors, it is probable that they are present in centipedes. If this is true, the validity of the experiments reported here and the hypothesis drawn from them are relevant.

The hypothesis that moisture is a limiting factor in the distribution of local centipedes centers about the series of desiccation experiments discussed previously. These in turn were augmented by earlier work (Auerbach 1949) in which three of the local species (*Bothriophis multidentatus*, *Neolithobius voracior*, *Otocryptops sexspinosus*) responded differen-

tially in a humidity gradient. Similar experiments in the present investigation yielded confirmatory evidence (Tables 4, 5, 6). It was felt that the time of survival under conditions of desiccation might yield results bearing on this hypothesis.

The experiments indicate but do not prove that there is a different survival time to desiccation conditions as between centipedes. The reason that significant differences were not found in all controlled experiments may be that the relative humidity chosen (35%) was sufficiently high to permit significant survival of two or more species. Further evidence of this is indicated by the results of the desiccation experiments using the petri dish method. Here the relative humidity used was close to the room relative humidity. The latter, particularly when the radiators were in operation, ran about 20%, but on occasions the relative humidity was higher. The curves of survival (Fig. 3) indicate a much greater difference between the species than do those of the controlled experiments (Table 8). What is needed is a set of experiments patterned after those of Gunn & Kennedy (1936), in which a centipede's critical relative humidity requirements could be determined.

The present experiments are not critical in an absolute sense but they tend to support the hypothesis of the zoogeographic distribution of *B. multidentatus*, *N. voracior*, and *L. forficatus* as observed in the field. *B. multidentatus* had the shortest survival time and is found in the most mesic forests. *L. forficatus* is found in the xeric environments and had the longest survival time. *N. voracior* reaches its greatest species population abundance in environments intermediate between the above two, and has a survival time that is intermediate between *B. multidentatus* and *L. forficatus*.

The results obtained with small centipedes of prairie and forests were different. The forest species in both sets of experiments outlived prairie species of about the same body size and weight (Tables 7, 8, 9). This was true for both the Lithobiomorpha and the Geophilomorpha. Two explanations are that something in the habitat relations of the animals may account for this survival differential, or the experiments are at fault and the results are less meaningful. The prairie species, *Pokabius bilabiatatus*, *Areophilus bipuncticeps*, live on or in the ground between the stems and roots of prairie plants. The forest species, *Sonibius politus*, *Geophilus rubens*, live chiefly under bark. In the case of *G. rubens* the bark niche need not be wet. We have taken them under the bark of dead, dry trees. During midsummer the prairie species are almost unobtainable. The animals burrow deep in the ground. Thus we have a differential in natural environments that possibly is expressed in a differential sensitivity.

POPULATION INVESTIGATIONS

The prairie species apparently are more sensitive to changes in local weather than are their forest allies (Figs. 7, 8). For example, they may execute vertical movements through the prairie floor and subterranean stratum in response to relatively small

changes in microclimate. Although many workers agree that moisture is the most significant factor in controlling abundance and migrations of the majority of soil organisms (Pearse 1946), such emigrations may be rapid but are not fully understood in the present inadequate condition of our information. This sensitivity is expressed in another way, i. e., in a lesser ability of prairie species to withstand desiccation as compared with the forest species. These latter occupy niches the relative humidity of which is relatively constant throughout the year.

In spite of the prairie species being more responsive to general climatic conditions their average population density (Table 10) is almost twice that of Carlé Woods, namely, twenty-seven per square meter to fourteen per square meter respectively. There are at least two explanations for this difference in community population density. One, the Nearctic grassland environment is richer in soil organic materials than most Nearctic forests (Blumenstock & Thornthwaite 1941). Grasses with their thick underground root systems and their high mineral content build up a rich soil more rapidly than this process is accomplished in forests. This should be readily apparent to any who has fingered the rich, black prairie soil of midwestern United States and the thin, sandy forest soil of the same area. Carlé Woods has a thin leaf mold of about an inch in thickness. This is much less than the litter found in the Beech-Maple and Hemlock-Hardwoods communities. If the prairie soil had been compared with the humus and soil of a Beech-Maple climax forest such as that at Lakeside, Michigan (Warrens Woods), entirely different results may have been forthcoming.

Too, Carlé may have been inadequately sampled. The logs maintain a considerable centipede population which fluctuates at various times of the year. Two dozen centipedes can be taken from a stump on a spring day while the leaf mold and soil rarely will contain that many animals in a given sample. At other times of the year, a part of the log population may move into the forest floor particularly if the leaf mold is wet. The use of random sampling on such a transient group of animals, while admittedly in need of improvement, is probably the best method used at present. It must be borne in mind also that there is a large log and stump population that must be sampled by other means. In the final analysis Carlé Woods may have a higher centipede population than Pcaock Prairie.

With these general results in mind, if moisture is a factor that governs distribution, it apparently operates in at least two ways. First, centipedes that are forest inhabitants, and live within areas of reasonably stable relative humidity, are limited in their distribution, generally speaking, by their ability to tolerate, or not to tolerate, higher or lower constant relative humidities in their major environment. Thus *Lithobius forficatus*, which is found predominantly in open woodlots, under piles of debris, and under rocks, is in these niches since it is adjusted to meet the xeric conditions that are usually present at one or more times of the year. On the other hand, *Bo-*

thropolys multidentatus, which is occasionally found in arid environments, reaches its greatest abundance in the most mesic of forest conditions. *Neolithobius voracior* is found in conditions intermediate between these extremes.

Second, centipedes that live in the prairie environment, typified by extremes of wetness and dryness, are more sensitive to conditions of drying. This is indicated not only by their shorter desiccation survival time (*Pokabius bilabiatius* versus *Sonibius politus*; *Arenophilus bipuncticeps* versus *Geophilus rubens*), but also by two years of field observations and collecting. This increased sensitivity would tend to have survival value in prairie centipede populations in that it would stimulate them to burrow beneath the surface of the ground and out of danger of desiccation during the dry period. Forest species that live in a comparatively constant relative humidity are not as sensitive. Therefore, it is possible that forest centipedes do not penetrate the prairie environment, except in those cases where certain species possess the ability to respond quickly to changing conditions of moisture.

SUMMARY

The Chicago Area contains remnants of several forest types. These include Hemlock-Hardwoods, Beech-Maple, Red Oak-Maple-Basswood, Oak-Hickory, Black Oak-Hill's Oak, and Bur Oak forests. In addition prairie, which formed one of the important vegetation types in this area, is still represented by scattered patches of grassland.

Thirty species of centipedes representing twenty-one genera are at present known from these communities. The majority of these centipedes seem to be uniformly distributed. Exceptions to this include certain of the forest and prairie species.

Bothropolys multidentatus, *Lithobius forficatus*, and *Neolithobius voracior* are three of the common local centipedes. Their local distribution, on the basis of field work to date, does not follow a uniform pattern. *B. multidentatus* reaches its peak of abundance in wet forest communities, *L. forficatus* is most abundant in dry forest communities, while *N. voracior* is plentiful in those communities in which floor moisture conditions are intermediate.

The biology of some of the better known species is discussed. Oviposition in all the local species apparently occurs in June or July. Hatching occurs toward the end of August and early September. No evidence has been found as to when fertilization takes place since copulation has never been observed.

The rôle played by humidity in the distribution of Chicago Area centipedes was investigated. An experimental approach that involved the subjection of various species of centipedes to conditions of desiccation was utilized. Using the petri dish technique, the three species mentioned previously had a mean adult survival time of 4.0 hours (*B. multidentatus*), 5.9 hours (*N. voracior*), and 9.3 hours (*L. forficatus*). The small prairie *Pokabius bilabiatius* had a mean survival time of 2.4 hours, while the small forest

Sonibius politus had a mean survival time of 2.7 hours.

These and other species of centipedes were subjected to desiccation in constant humidity chambers. The results were not as unequivocal as in the first set of experiments, but the trends were substantially the same. *B. multidentatus* had a mean survival time of $5.4 \pm .44$ hours; *N. voracior*, $5.5 \pm .18$ hours; and *L. forficatus*, $6.6 \pm .40$ hours. *P. bilabiatu*s had a mean death time of $2.4 \pm .11$ hours while *S. politus*, the small forest form, still had a significantly greater survival time of $2.7 \pm .13$ hours. Similarly the prairie geophilid, *A. bipuncticeps*, had a mean survival time of $7.3 \pm .36$ hours, while the forest geophilid, *G. rubens*, had a mean survival time of 27.8 ± 1.7 hours.

According to the Spencerian principle of surface-volume relationships the larger species would tend to survive desiccation longer than the smaller species. This is borne out in centipedes when body length is used as a criterion of size.

The evidence suggests, but necessarily does not prove, that the three common lithobiid centipedes (*B. multidentatus*, *N. voracior*, and *L. forficatus*) that live in stable forest environments, survive in the desiccation chamber in inverse proportion to the moisture level in their natural habitats. For example, *L. forficatus*, which lives in more arid niches, survives longer in the desiccation chamber than does *B. multidentatus*, which is typical of moist habitats.

Prairie species that are subject to sudden and great fluctuations in moisture during the year are, on the other hand, more sensitive to humidity than forest species in the same size category. This sensitivity would have survival value in that it would serve to drive them below the surface of the ground and out of danger of desiccation during a dry period. Forest types that live in a relatively stable humidity through the year would not necessarily have evolved such a sensitivity. Natural selection probably operates here at the community level.

Weekly Berlese samples were taken in Carlé Woods, a Red Oak-Sugar Maple-Basswood forest, and in Peacock Prairie, a tract of undisturbed grassland. The average monthly populations of centipedes were examined in relation to the average mean air temperatures, total precipitation for the periods preceding each collection, and soil temperatures taken at the time of sampling. There is a reasonably close correlation between spring and autumnal peaks in the prairie centipede population and local weather. Carlé Woods did not show a decided peak in abundance of centipedes in the spring. Instead, the increase in March continued as a plateau of abundance through May. The insulating effect of the forest canopy may be one of the underlying causes of this phenomenon. The prairie centipede population was always larger than the forest population. Two explanations of this situation are offered, namely, that Peacock Prairie is richer in soil organic materials than is Carlé Woods and consequently can support a larger invertebrate population, or that log centipede populations of Carlé Woods are not represented in the Berlese samples.

A series of boards were placed on the ground of Peacock Prairie. These were turned over every week and the numbers of centipedes observed and recorded, as well as the general moisture conditions of the boards noted. For the period of study, the centipedes under the boards did not conform to a Poisson distribution but rather formed a "contagious distribution" (Cole 1946a, b). Evidence is presented that indicates that this non-random distribution is not an aggregation due to mutual attraction, but is a response to certain environmental factors, among which moisture would seem to be important.

Heart-beat rates of various local centipedes were taken. A comparison of these rates indicates that there is a species difference in rate of heart-beat. The Q_{10} of a few of the local species was calculated. It varied from 1.43 to 3.77. Heart-beat rates in centipedes can be used for this type of experimentation as the hearts are easily seen and heart-beat variation in relation to temperature is easily obtained.

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